ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

VOLUME VII

MARCH 25, 1926—1931 DECEMBER

NUMBERS 1–5 INCLUSIVE

PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

New York Zoological Society

General Office: 101 Park Avenue, New York City

* Deceased

TITLES OF PAPERS

LIST OF ILLUSTRATIONS

THE THREE-TOED SLOTH

Figures 1 *to* 23 *inclusive*

DEVELOPMENT OF SOLDIER TERMITES

Figures 24 *to* 32 *inclusive*

A NEW POLYCHAETOUS ANNELID

Figure 33

A RIVER DOLPHIN FROM KARTABO

Figures 34 *to* 45 *inclusive*

THE REDUVIIDAE OF KARTABO

Figures 46-47

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

DEPARTMENT OF TROPICAL RESEARCH
KARTABO, BRITISH GUIANA

VOLUME VII. NUMBER 1

Department of Tropical Research Contribution Number 228

THE THREE-TOED SLOTH

Bradypus cuculliger cuculliger Wagler

By William Beebe

Contributions to the Life History and Anatomy of the Mammals of Kartabo, Bartica District, British Guiana

PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

March 25, 1926

New York Zoological Society

General Office: *101 Park Avenue,* New York City

Zoologica Vol. VII, No. 1.

THE THREE-TOED SLOTH

Bradypus cuculliger cuculliger Wagler

By William Beebe

Contributions to the Life History and Anatomy of the Mammals of Kartabo, Bartica District British Guiana

(Figs. 1–23 incl.)

OUTLINE

Introduction

There are two species of sloths found at the Tropical Research Station of the New York Zoological Society, Kartabo, British Guiana. These are the Three-toed Sloth, *Bradypus cuculliger cuculliger* Wagler, and the Two-toed Sloth, *Choloepus didactylus* Linné.

Fig. 1. Head of adult male three-toed sloth. From a water-color drawing by Isabel Cooper.

Reserving an account of the latter for a future paper, I present herewith the results of my observations on the Three-toed species. This edentate was named in 1831, but very few observations have been made upon wild or recently captured specimens during the ninety-five years since that time. Upon this particular Guiana form the literature is almost nil, and I have summed up near the end of the paper all the published data I could discover worthy of quotation.

The paucity of notes on the three-toed forms is the more readily understandable when we realize that these animals, unlike the two-toed sloths, will not accept a change of diet in captivity, so while they feed freely and thrive within reach of their wild food plants, they will not survive transportation to northern Zoological Parks and Gardens. As regards the viability of *Bradypus* in confinement my own note of eight months at Kartabo seems to be a world's record as compared with one month in the London Zoo and three in our New York Zoological Park. On the other hand, the two-toed Hoffman's sloth, of which I shall have more to say later, adapts itself philosophically to captivity, and shows a record of nearly four years in New York and over eleven years in the London Zoo.

My notes on sloths are based both on careful studies and casual notes made at Kartabo, British Guiana in the research area of the tropical station, the observations being carried on over parts of several years, and including every month in the year. The individuals in confinement lived in semi-freedom on several good-sized trees on a terrestrial island, surrounded by a deep, three-foot wide, dry moat, which proved an impassable barrier. Old and young of both sexes have lived here for months, feeding, climbing, sleeping, courting, caring for their young, and in general living normal lives, except when I have removed them for swimming tests and other experiments. Some have escaped into the neighboring jungle, a few have died from special, interesting causes in no way connected with the conditions of their confinement.

Detecting and Collecting Sloths

Sloths have no right to be living on the earth, but they would be fitting inhabitants of Mars, whose year is over six hundred days long. There are only two similes in the world to which they may satisfactorily be compared, first, the Rath Brother acrobats, and second, a slowed-down motion picture.

The first time I saw a sloth it was a bunch of vegetable para-

Fig. 2. Male three-toed sloth, showing great length of fore-legs and powerful tail which is useful in climbing. Photograph by Elwin R. Sanborn.

sites, the second time it was a white ants' nest. At least that is what I supposed these were, but when I looked for them again, they were gone. The third time I saw a sloth, it was in a high tree. I fired at it and blew down a whole shower of roots, moss and stinging ants. From this time on I never called anything a sloth without shooting at it, or more frequently, watching until it moved.

To the sloth-seeker I can only say that no tracks or forms are visible, no hollow or nest offers a clew, and it is almost as hopeless to listen for its voice. I have found three ways of successfully procuring these animals, first, by sheer search, covering reasonably open jungle and river banks, scrutinizing every suspicious, dark, rounded mass in the branches; second, by going after every creature swimming in the rivers, on the very reasonable assumption that it may be a sloth, third, to notify the Indians and other natives to bring in all the sloths which they find among the branches of trees felled in making their cassava fields. Once I tracked a sloth by its voice, and twice by sign, but these are rare feats of superlative woodsmanship, or more honestly, pure luck or accidental flukes.

Brief Description

The senses of the Three-toed Sloth being of an exceedingly low order of development, there is little need for a face except as an ingesting focus. The head is round, hardly differentiated from the remarkably long and mobile neck, while the face is as simple as the face of a mammal could well be. The body is thick-set, short, and with great mobility of the vertebral column; the arms are slender and very long, a full third longer than the legs; the tail is short and stubby but a very useful organ.

The whole animal is covered with long, coarse, but strangely soft and silky hair, which serves as thatch in rain, and, with the dense under fur, as a real protection against the attack of many foes. The general color of this species is a grizzled drab, with irregular patches of dirty white on the dorsal surface. The males are highly colored for mammals, having bright orange ear patches and a rounded spot of the same color in the middle of the back. Very rarely an adult female sloth in the pink of condition will have dull orange ear patches, but never the brilliant back marking.

Abundance

Difficult as they are to discover, Three-toed Sloths are decidedly

Fig. 3. Sloth tree at Kartabo, isolated by a dry moat, where many of the observations in this paper were made. Photograph by John Tee-Van.

common animals within the research area, and they are doubtless even more numerous than they appear to be. During two years, when the square mile about Kalacoon was being cleared of primitive jungle, fourteen sloths, four of which were carrying young, were found among the branches of the felled trees. This was before the opening of the Research Station. At Kartabo and the immediate vicinity I have notes on twenty-eight Three-toed Sloths, four of which had young, and two others large embryos.

If we take the agouti as the most abundant mammal of Kartabo, and the spider monkey as a type of the rarest, Three-toed Sloths must be classed as common. By the same criterion the Two-toed Sloth would be decidedly rare. I believe that this would hold good for most of the interior of Guiana, while I have found a closely related form of the three-toed type to be actually abundant along the lower Orinoco. As to past history it is interesting to record, of this very region, that in the year 1876, Dr. W. T. Hornaday shot eight sloths from a dug-out along the west shore of the Essequibo, from Groete Creek to the mouth of the Mazaruni. Within a square quarter-mile of research area I estimate there are at least twenty resident Three-toed Sloths. I have seen three of these, and have captured several others, not counting those which have swum ashore.

Haunts

Sloths are lovers of river banks, and I can recall only one individual which I have seen more than a mile inland. In spite of the succeeding section, the attraction is probably not the water itself, but the more open character of the jungle, and probably the abundance of food plants.

One of the most remarkable phases of the sloth's history is the readiness with which it takes to water. We have photographed a sloth coming ashore; I have thrown sloths into the river far from shore and watched them make their way to land, and altogether we have captured twelve sloths swimming in mid-river or taken them from islands where they had recently stranded. Kyk-over-al, the historic Dutch island, four hundred yards from our laboratory, and over five times that distance from the opposite bank, has provided four sloths, although it has only a few small trees wholly unsuitable for sloth food.

In every case which I could verify, the direction has been south or west, and, like the migration of the Catopsilia butterflies, the

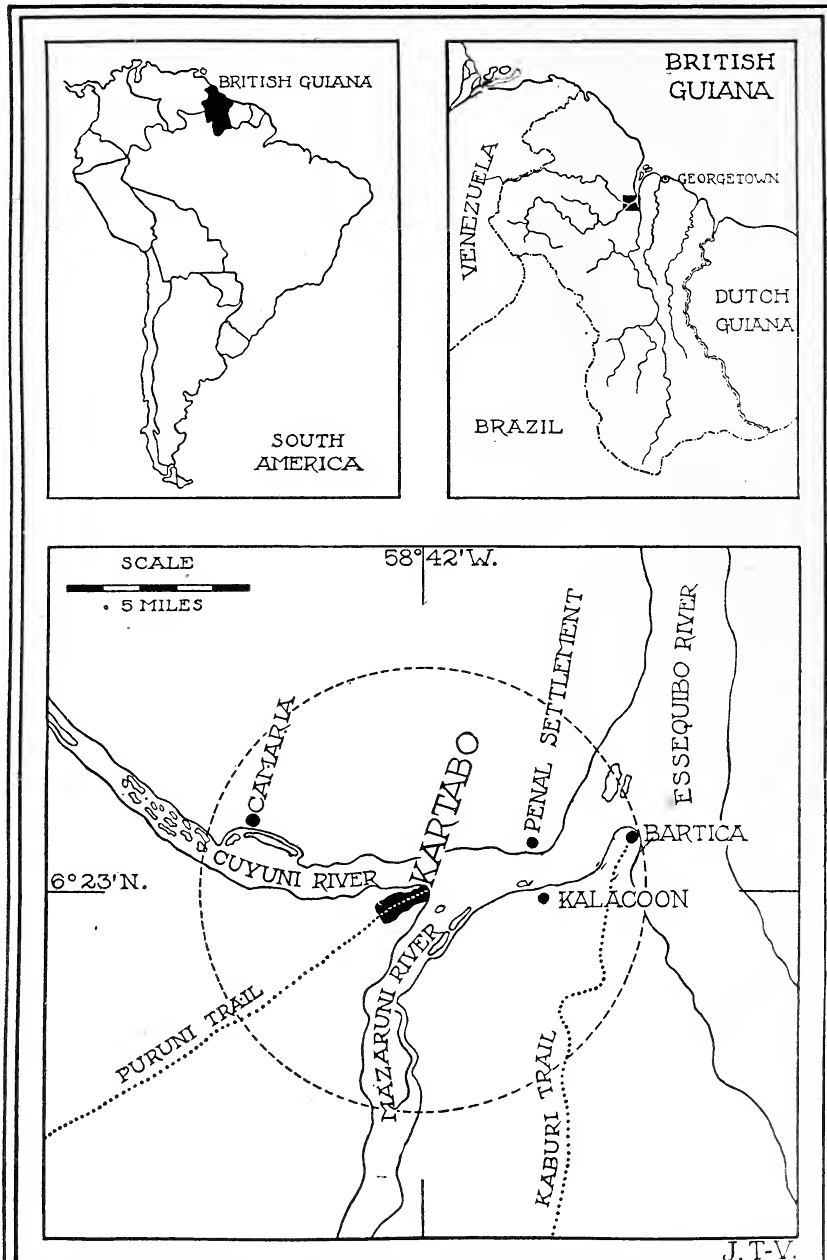


Plate A. British Guiana Tropical Research Station of the New York Zoological Society. Circle represents a radius of six miles.

Drawing by John Tee-Van

Fig. 4. Sloth carried by seizing the hair in the middle of the back, the only way to avoid the sharp claws. Photograph by John Tee-Van.

reason wholly beyond my ken. The season of most abundant migration is the early part of the long wet season in May and June. There are few large voracious fish which could bite through the thick fur and skin, but crocodiles are far from absent and the tide and current are often much too strong for the sloths to swim obliquely across even at the most favorable times. Every sloth must be carried one or two miles down-stream in its trans-fluviatile progress. I am quite certain that none of these swimming sloths has fallen by accident into the water, for they know rotten boughs almost by instinct, and if they did fall in, they could if they wished climb out again at once. There is some urge, some powerful instinct, which brings these ultra-arboreally specialized animals down from the trees and out into vast expanses of water, with the opposite shore wholly unknown and quite invisible to them. The cause is certainly not due to lack of food or mates, or any disturbance from mankind. Like their distant relations, the great ant-eaters, they take frequently to water and that is all that we know about it.

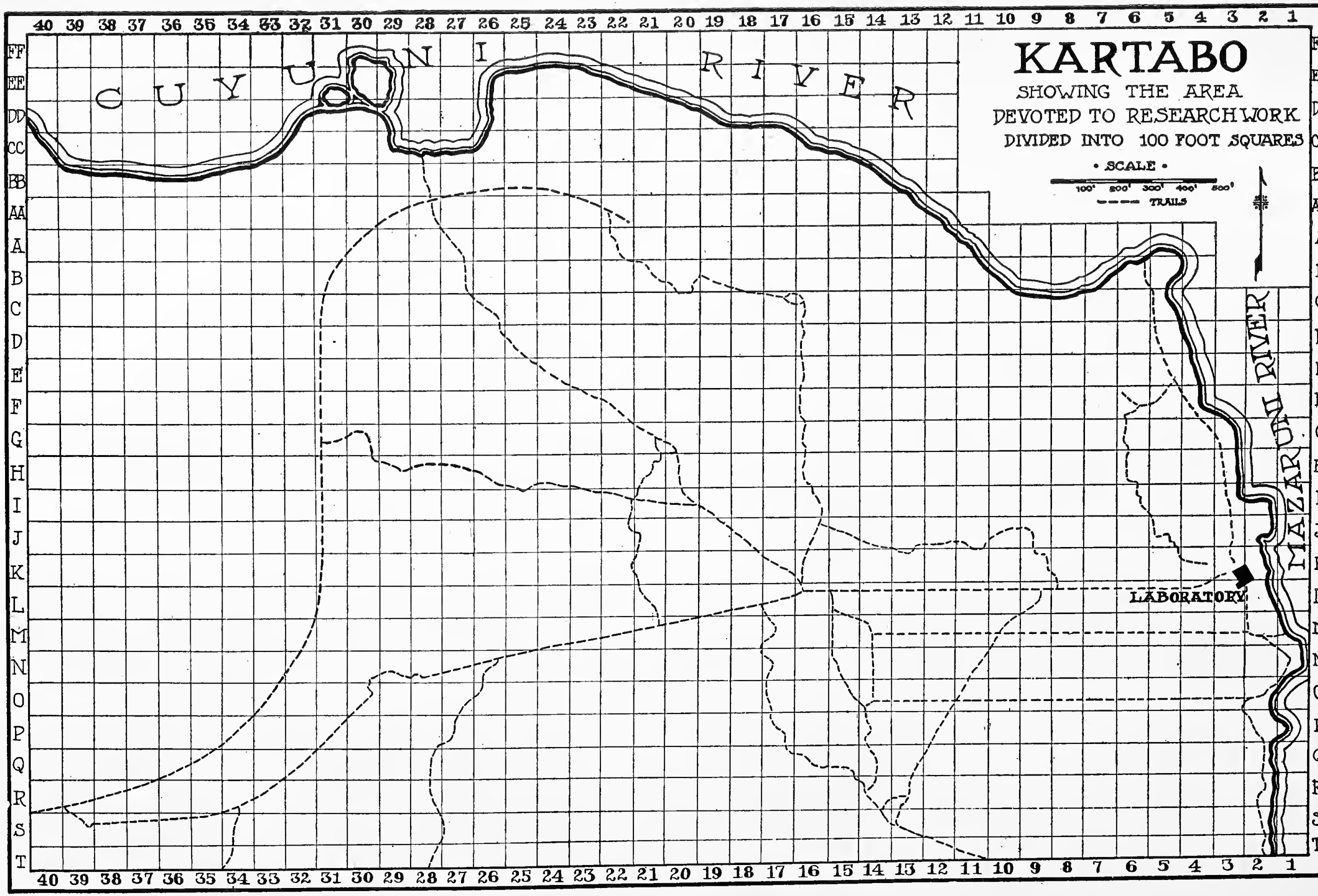


Plate B. Area devoted to research at Kartabo.
Drawing by John Tee-Van.

Migrations

Except for these unaccountable departures and arrivals, sloths are as resident as the abundance of their food plants will permit. More ideal subjects for banding would be difficult to imagine, but whenever I have captured one I have usually wanted it for the Zoological Park, or for a specimen, and have only once marked a sloth. This was of interest, however. The sloth, a nearly full-grown male, had just swum ashore at Kalacoon, coming from upstream on the Penal Settlement side, three-quarters of a mile across the Mazaruni. After keeping it five days, I shaved two patches of fur from the sides of the back, on the edge of the orange dorsal spot, and tied a metal tag to its leg. I liberated it in the jungle back of Kalacoon, and forty-eight days later it was brought to me from Ororaibo, a clearing with a few thatched huts on the west bank of the Mazaruni. To reach this place it must have gone west to the river bank from the mile inland where I liberated it, then turned south-west and taken to the water about two miles further up-river, then swum a mile west and down to the spot where it was seen to come ashore. The metal tag was gone but the shaved spots were unmistakable. The total distance was at the least four miles of jungle and one of river. Allowing a single day for the latter feat, we have an average of about one hundred and fifty yards of direct travel for each of the remaining forty-seven days. As there was a full moon during the interval it is probable that the animal made much of its progress at night. But two wide rivers and four miles of jungle, with an interval of only five days' rest in captivity in less than two months is almost enough to redeem it from being the type of inertness and laziness. Of the twelve sloths observed swimming the river, nine were males, and three immature females.

While this general seasonal shifting of certain individuals is apparent, the home range of these animals is more obscure. The old stories of a sloth spending its whole life on a single tree or never leaving it till every leaf is eaten is, I am afraid, pure fiction. For five days I have kept track of a female sloth which fed on three adjacent cecropia trees, and every night went back to the identical crotch of a dalli tree to sleep. She then vanished and a thorough search of the adjacent open jungle failed to reveal her whereabouts. It is probable that sloths are restless creatures and keep more or

Fig. 5. Three-toed sloth creeping painfully to the nearest tree. Photograph by William Beebe.

Fig. 6. Three-toed sloth climbing a cecropia tree. Photograph by William Beebe.

less on the move, but I believe that usually their wanderings are rather limited, and the adult sloths often spend most of their lives, or at least several years, in the same limited area of jungle. Besides several reasons which I shall elucidate later, I base this belief on the extreme regularity of their habits in captivity, and the routine tendency apparent, whether the animal be confined in cage, vivarium or large enclosure.

Sociability

I have never seen even two sloths together. Once I saw two within a hundred yards of one another, but it might have been a hundred miles for all the knowledge they had of one another's presence. They are decidedly solitary animals and, as we shall see, the general law of relationship between sociability and voice holds good with them as with birds and other animals.

I have studied sloths for many years and have watched them for weeks in captivity. At this moment I have within a few feet, a three-quarters grown male, and two tame mother sloths, with a one-week, and a four-week old baby, respectively, yet psychologically, unless I brand them as being below reptiles and many amphibians, they are either a mystery or are beyond belief simple and dull; which is perhaps another way of saying that I am not able to put myself in their position and get their point of view of life. Still I am not so bad as Buffon, who chose sloths as the types of imperfection in nature, and wrote, "One more defect and they could not have existed." A sloth in Paris would doubtless fulfill the prophecy of the French scientist, but on the other hand, Buffon clinging upside-down to a branch of a tree in the jungle would expire even sooner.

Certain reactions of sloths to captivity, while they should be kept sharply distinct from the activities of animals in a state of freedom, yet possess a decided significance when exhibited consistently by all individuals. There is an interesting sequence of temperament through which all sloths pass when captured and placed in a cage. At first they show the resignation to fate characteristic of the free animal when approached on their native branch. They roll up, hide their heads, and wait for the blow to descend, or to pass. After a few days when there comes to their dull comprehension the fact that my presence does not mean physical harm, they begin to move about freely and to feed, and with this phase is correlated a pacifistic resentment of my approach, and instead of cringing, they make futile attacks with their fore claws, and then climb slowly away.

After two, or with some especially dull individuals, three weeks, the sloths become tame, and will come for food when it is brought, will allow themselves or their young to be stroked, exhibiting day and night, the eternally characteristic emotion of the race of Three-toed Sloths, that of passive tolerance.

Specific Individuality

Habits are formed very quickly, and when a satisfactory roost is chosen on one night, it is resorted to without hesitation the next and thereafter. Food location is also fixed in mind after a single feeding. In a small cage when a newly caught sloth has once made an escape, as between the wire and the ground, the occurrence is not forgotten. The animal will sprawl flat and continue its efforts at escape, even in imminent danger of crushing its young, for several hours each day, writhing about on the bottom of the cage and poking blindly against the wire with its head. If removed to a new cage for a few days, and then returned, all memory of the happening is gone.

Dully tolerant as sloths are of whatever life or fate may bring, they are extremely intolerant of one another. If several are placed on a large tree for observation, one will always make it uncomfortable for the others, but in a small cage it is as good as murder to put two sloths, especially if they be females, together. Males, or a male and a female, will usually live grudgingly together, giving one another occasional hooks with their claws, but two female sloths present the most unpleasant sight imaginable. After a brief sparring, one gives up and flees and never after attempts to defend herself. The other may for a time languidly feed, or sleep for hours, but it never forgets its companion, and sooner or later it climbs slowly to the hunched-up unfortunate, and deliberately begins to inflict as much damage as possible. Hook after hook is made, and the mysterious part is that the persecuted sloth permits herself to be unrolled and systematically clawed, a single swing sometimes tearing part of the tender skin of the nose. Wailing at each attack, the hopeless creature lets go and lies flat on her back, with all her vulnerable parts exposed, apparently awaiting death at the hands of her fellow sloth. The attacker tries now and then to bite, usually vainly. Only once I saw one get hold of a hand instead of a mouthful of hair, and from the way it was wrenched and from the ensuing wail, the flat teeth must be able to cause considerable pain. I have never

allowed such an attack to continue, it is too horrible, and I know of no other mammalian conflict which is so abhorrent. The idiotic, emotionless faces of the sloths, one emitting a series of plaintive wails through the nostrils and without attempting either to ward off blows or to retaliate; the other slowly and systematically setting to work to destroy her sister;—this is decidedly the least attractive side of sloth life.

Movement

Every muscular movement, sensory reaction and mental process is slowed down in these animals; their lives are spent wholly in low gear. They are the personification of slow deliberation, and only from an anthropomorphic bias can they be termed lazy or slothful. A turtle shows sometimes the slow, deliberate movements of these mammals, or a heron stalking a fish; a chameleon also in its syndactyle climbing; but turtles or herons can hurry if they choose, while to a sloth, haste is inconceivable. When, however, a sloth lifts itself from branch to branch, drawing its whole weight upward with three fingers and no effort, or, stretching far across an open space, brings body and legs after without shock or swinging impetus, one is forced to admiration, as in the supremely graceful, effortless feats of superlative acrobats, or the analysis of movement of some animal in swift action in a slowed-down motion picture.

A jerk or sudden movement is unknown to a sloth between birth and death. The nearest approach is what pugilists would call a short-arm hook, with which the sloths endeavor to defend themselves, and the exertion of this is so great that if they miss the object aimed at, the impetus often completely upsets them.

In connection with exertion it is interesting to note that a sloth breathes about once a second, but very irregularly. An average of several trials gives twenty breaths to sixteen seconds. After swimming nearly one hundred feet, and being angry into the bargain, a sloth breathed twenty-five times in twenty-five seconds, most of the exhalations carrying a hissing grunt, an involuntary, non-vocal protest against my holding him. The temperature of an adult female sloth was 95½°.

The human failing of exaggeration in the estimate of speed is as evident in the case of slowness as of rapidity. A race horse may seem fairly to fly over the ground, until pulled down to the actual record by a stop watch, and to all the earlier observers, the fact of

the unusual slowness of sloths led to the most ridiculous estimates of their speed.

A mother sloth on the ground, speeded up by the calls of her infant, made fourteen feet in one minute, and while I have known this to be considerably surpassed, yet it is a fair average of twenty tests made with half as many animals. This corresponds to a mile in six and a half hours. In the trees this speed may be increased to two feet a second. The most unexpected record of a sloth's activity is that of swimming. An average is the feat of a male, not particularly vigorous, which swam sixty-five feet to the nearest bush on shore in two and a half minutes. This is one foot in two and a third seconds, which is to say that, ignoring all contrary currents and tides, a sloth, keeping up this rate of progress, could cross a mile stretch of river in three hours and twenty minutes.

A sloth swims remarkably high out of water, three-fourths of the head and much of the back being exposed. Even when thoroughly soaked, considerable of the back is above the surface. The strokes are made at the rate of one to three-fourths of a second and almost all the propulsion is with the front legs. These swing around alternately on each side, nearly to the tail, while the hind legs and the posterior half of the body waggle feebly from side to side, to meet first one, then the other backward-coming front leg.

The mobility of the neck and forearms of sloths is almost that of universal joints. When we remember the necessary rigidity of the limbs of running animals, we realize that a deliberate and an arboreal life has its characteristic compensations.

The head and neck can be, and in sleep always are, brought forward and around until they are flat on the breast. When needful, the neck can be stretched back in the opposite direction, until it is below and at right angles to the longitudinal body axis. This indicates a superior-inferior swing through an arc of 270°. From a normal position parallel with the vertebral column, the head and neck can be revolved laterally to an equally surprising extent, three-fourths of a circle. For example, if the sloth, while in an upright position, is looking north, it can slowly turn its head to the right, through east and south, to west and on even somewhat farther, to west by north.

The elbows can be brought together in front and behind the body, over the head and down across the abdomen. With the lower leg pointing tailward, the knees cannot be brought closer together in

front, than parallel, nor when stretched laterally can they be brought further back than a straight transverse line. Posterior to this line they will go only a short distance. Thus there is a very great degree of difference between the mobility of the fore and hind limbs.

When the lower legs are brought inward across the abdomen, however, the upper limbs approach somewhat nearer, 65 mm. instead of 85 as in the first instance.

When stretched straight out laterally, the hind limbs can be rotated tailward until they touch, thence allowing an anterior revolution of 180° until they lie alongside the body. When thus stretched forward, the tip of the foot falls short of the armpit, reaching the mammary glands.

The forearm can be revolved upon the humerus through a half circle; if the arm is stretched out laterally, with the palm upward, it can be turned so that it faces directly forward and as completely back. The lower legs and the soles can turn only about 45° in either direction.

With the forearm in the same position, the hand can be bent back at a right angle and forward three-quarters or 70° of the way to the forearm. It can be rotated almost at a right angle (80°) posteriorly, but only 40° forward. The claws can be stretched straight out, and flexed through 180°, until they touch the palm. The hands and feet, together with the claws, are practically immobile except in an externo-internal direction.

The body can be rolled up until the back is in a perfect ball, and the nose touches the tail-tip, but a backward bend is an impossibility. There is almost always a curve in the lower back, about sufficient to compensate for the disparity in length of the hind as compared with the front limbs.

The tail is very short, thick, rounded, and tapers rapidly with an abruptly outward curved tip. It is very mobile, and will pass dorso-ventrally through an arc of 180° and laterally through 134°. While this movement is chiefly basal, yet even the tip is movable. This lateral portion is covered so densely, and with such short, thick hairs that it appears bare.

It is a mistaken idea that sloths spend all of their lives upside-down. When travelling and often when feeding, they do hang suspended, but quite as often they are climbing or clinging on vertical stems, or actually sitting down, as when asleep. On the other hand it is physiologically impossible for them to stand upright on

Fig. 7. Mother and baby three-toed sloth, showing method of carrying the young when the parent is in motion. Photograph by William Beebe.

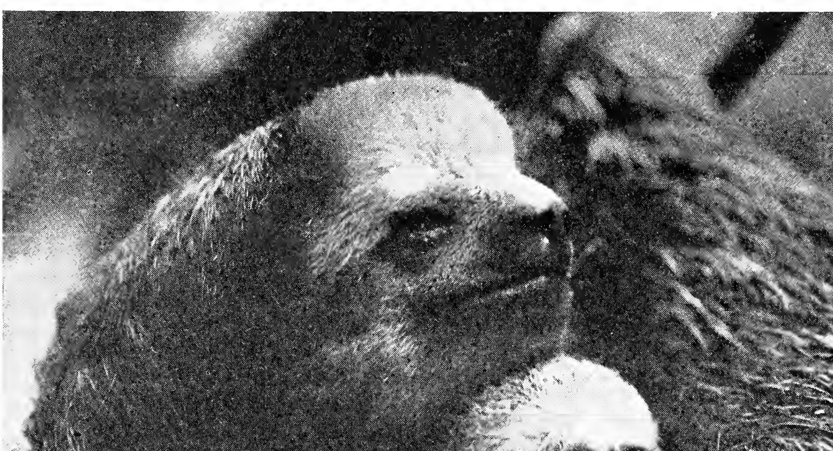


Fig. 8. Mother and baby three-toed sloth. The parent is beginning to wrap her body and limbs about the infant to protect it from danger. Photograph by William Beebe.

all fours either on the ground or at least for more than a moment on the branches. I have thus modified this last statement because of the achievement of a newly caught male sloth. This animal, when liberated on my sloth tree, climbed at once to the top, and then, eager to reach the bamboos above him, which his poor eyesight failed to reveal as still twenty feet beyond the reach of his claws, he actually stood *upright* on the topmost branch. He gripped it tightly with all four feet, and for a few seconds, held himself quite at full leg length, the strangest sight I have ever seen in my studies in slothdom.

To get a better view I walked beneath him, and when he saw me, he relaxed onefoot-hold and slid at once down to normal sloth attitude. He then let go with first one, then the other forearm, and even one hind foot, and stretched far down toward me, seeing in me the hope of another tree. Everything that comes near a sloth is Birnam Wood to him.

When hanging, the support of the species under consideration is usually wholly the twelve claws: when climbing, the feet are brought into play, the elongated tarsals and metatarsals of the front foot, and the corresponding series, aided by an extremely elongated calcaneum in the hind foot, forming with the claws a peculiar type of syndactyle grip which is perfect in its adaptation to its requirements. The claws can be straightened out, as when reaching for a branch, or hooking over the ground. The reported danger of being caught in the grip of these is imaginary, for while they can give a severe pinch, they cannot cut through the skin unless an attempt is made to tear the hand away. The curving slice which they give occasionally is a different matter and can inflict a deep cut. Their method is slowly to strike forward in the direction of the enemy and then bend backward, curving the arm around with claws half flexed.

Defense

When fully enraged, having mentally attained the emotional level of annoyance of other wild animals, male sloths will, at this stage, slowly reach forward with the head, open the mouth and attempt a languid bite. I have known one to bite its own wrist, mistaking it for my hand. I have not experimented with the efficiency of this mode of assault, but probably if given time and perfect convenience of grip they could chew enough to do considerable damage. Such defense is pitiful against the swoop and talons of a harpy, or the claws of a cat, or the crushing coils of an anaconda.

Every Three-toed Sloth has its individual expression, but this never changes under stress of emotion, hunger, anger, sleep, even when nearly drowned after a mile of swimming, always there is the same, humanly-speaking, smug, wide-eyed, vacant outlook upon life. In what the sloth conceives the last extremity, there comes a shrill, heart-rending whistle through the nostrils, accompanied by not the slightest quiver of muscle or shifting of feature.

Senses

The senses of sloths are of great interest from their simplicity. In the order of progressive efficiency I should name them taste, touch, sight, hearing and smell, and using the arbitrary range of II to X, to express respectively unusual dullness and extreme acuteness, I offer the following:

	II	V	X
Taste	Sloth	Dog	Man
Touch	Sloth	Man	Electric Eel
Sight	Sloth	Man	Eagle
Hearing	Sloth	Man	Deer
Smell	Man	Sloth III	Dog

Interest in the strange life and ways of adult sloths and the disarming charm of infant sloths are very liable to obscure the real status of their mentality, and after experiences with animals and birds which dash themselves against their cages, or mope and perish from no reason which we can discover, we are inclined to be over-enthusiastic as to the philosophic acceptance of captivity by sloths. But when we divorce from the question of their psychology all sentiment and false tameness, we are face to face with the fact that they have achieved a niche for themselves where they live, thrive and increase with the very least possible development and specialization of sensory perceptions and mental processes. Let me give a few concrete examples.

In the foregoing table I have neglected the level of I, because that would represent the very lowest, and feeble as are the senses of sloths, they are least clearly recognizable. As regards taste, only once or twice have I ever seen a sloth sample a leaf and then reject it. It invariably uses the sense of smell, and either turns away or begins feeding at once. However insipid may be the flavor of cecropia leaves, they never pall, and are detected and munched in preference to any other foliage of the jungle. Tests of touch have been made

when the sloth was asleep and it was quite on a par with taste; two or three nudges will awaken the animal and make it look sleepily in every direction but the right one. When wide awake and fencing laboriously, if a sloth is touched on the back, it will look up and down before it occurs to it to twist its wonderfully mobile neck and look behind. There is no delicacy in feeding; it simply munches until it reaches the base of the leaf and then starts on another, without any hint of feeling or touch.

The eyes of sloths are small, expressionless, very convex and round. In the adult the iris is of a deep tawny while in the young it is considerably lighter, more nearly a yellow ochre. They are only conspicuous because surrounded by a circle of black hair. In the young and immature animals, several rows of these are slightly lengthened and stiffened, forming very imperfect eye-lashes The eyes are placed above the level of the nares, and close to and exactly above the posterior corner of the mouth. They are directed forward with a divergent angle of about 25°, which in the young is reduced to 23°.

The pupil is exceedingly small, in daytime being reduced to a mere pin-point. Even at night, when a light is suddenly flashed upon the just-awakened animal, it is only about ¼ of the eye diameter. At death it relaxes to about half the diameter of the visible eye and changes to a wide vertical ellipse. The eye-ball is quite round, about 10 mm. in diameter. The eyes have very little power of revolution, and even when close to an object still keep their outward divergent angle, with almost no adjustment. The lids are close-fitting, and in the adult practically bare of eye-lashes. When wide open, the eyes are almost round, and the scantiness of eyebrows and lashes gives them a peculiar staring look. They are usually half or quite closed, however, and sometimes when feeding, they will remain closed for five minutes at a time. If a feint be made as if to strike the animal, instead of dodging, it will simply shut its eyes, lower its head and wait resignedly. Sloths wink frequently and very slowly, and as often as not, with one eye at a time. This adds to their general comical expression, the solemn, staring creature deliberately winking with right or left eye, the expression being as vacant as usual. One of the most inexplicable habits, especially when wet and drying off, is to nearly close the eyes, and half asleep, gaze directly at the sun for ten minutes to half an hour.

I have made numerous experiments with regard to the eyesight

of sloths, and can allow them no more than II, the imperfection of which may be gauged when we compare my comparative values of man V, and eagle X. Sloths are very short-sighted, so much so that it is impossible to think that this sense functions in any but the most unimportant way. It is inconceivable that sight is of the slightest use in finding food-trees, mates, or avoiding danger, at any but the very shortest distances.

It is interesting, as I shall detail later on, that there is a very appreciable ontogenetic change in vision. The very young sloths have better eye-sight, and shift their heads more in keeping with this improvement. Their eyes focus better, and unquestionably rotate inward, more toward an approach to parallel vision when looking closely at anything. The eyes are, as I have said, much lighter in color than those of the adults, and the pupil is comparatively larger.

Hearing in sloths is a worthy corollary of the voice. It exists, but that is about all that can be said of it. The ears are well back on the sides of the head, and measuring along the line of the mouth, they are just above it on a level with the eyes. The cephalo-nuchal mop or thatch of hair ends just above the ears, overhanging them. In the male these organs are the centre of a spot of brilliant orange, which extends a short distance in all directions, especially forward, and dies out about three-fourths of the distance to the eyes. The ear opens obliquely forward, is about as large as the eye, and roughly circular. The flap, which is all that there is of the tragus, is fastened posteriorly, opening forward, and must be of very little help in concentrating sound, being small, and useful only in closing the ear in case of need. The whole organ is completely buried and concealed in rather short but dense hair.

I have fired a gun close to a slumbering sloth, and to one feeding, and aroused but little attention. This is perhaps due, not so much to deafness, as to total lack of interest in such a noise. I am able at any time to attract the attention of any sloth by giving the characteristic plaintive whistle, although the reaction is of a most languid character except in the case of separated mother and offspring. I have watched sloths when a hawk was flying low overhead, screaming loudly, and neither sight nor sound penetrated the dull aura of mental opacity which invests the senses of these mammals. Again I have known the sense of hearing gradually to assume dominance in a feeding routine. Every morning a tall shoot of cecropia was cut and placed in the enclosure, and the sloth, asleep near the top of his tree,

would awaken and come down for his breakfast. When I took a particularly large branch, with juicy sprout and new leaves, very quietly to the tree, the sloth would sleep on for another hour or two before he woke, the odor evidently being impotent during sleep. When I came with the usual noise and in place of the tree, elaborately planted a rake, the sloth came down as usual, and went through all sorts of painful acrobatic feats before he succeeded in climbing within reach of the prongs, only then, by placing his nostrils close against them did he learn that it was not the cecropia he had expected. A sound, fraught with gastronomic memories, had aroused him, muscles and sight led him to the usual place, but neither sight nor smell, operating in unobstructed sunlight through a distance of from twelve feet down to one foot, served to save the sloth all the trouble of a difficult climb, and a final narial test at a quarter of an inch distance, of barren iron prongs. For five minutes the sloth clawed at the prongs and stretched his head helplessly in all directions, and then, as if overcome by the unusual mental effort, hung himself in the nearest crotch and went to sleep. Such reaction, in the face of wholly inexplicable and complete disappointment, has something amiable in it, from the human viewpoint.

The sense of smell is the only one to which I feel inclined to allot more than a II, and even here III is all that sloths deserve. Even this, however, is more than man can boast, who rightly sinks to II. I placed a sloth, hungry and not too disturbed, on an open area under the bamboos, and planted four shoots twenty feet away in the four directions of the compass. One of these was cecropia, camouflaged with thin cheesecloth, so that the best of eyesight would never identify it, and placed to the south, so that any direct wind from the east would not bring the odor too easily. The sloth lifted itself and looked blinkingly around. The bamboos thirty feet above, silhouetted against the sky, caught its eye, and it pitifully stretched up an arm, as a child will reach for the moon. It then sniffed with outstretched head and neck, and painfully began its hooking progress toward the cecropia. Variations of this yielded complete confirmation of the ability of the sloth to detect its food-plant at a considerable distance by the sense of smell.

Not only is each food leaf tested with the nostrils, but each branch, before the full weight is brought to bear. Again and again I have seen sloths draw back and choose another route, after a moment's close sniffing at a branch, which I invariably found was

decayed, and scarcely, if at all, able to support the animal, although to my eyes it might appear as strong and sound as the one the sloth was on. This is undoubtedly one of the most important requirements in its lifetime, and the existence or extermination of these animals might well rest upon the proper functioning of the sense of smell in this matter of detecting sound and rotten branches.

The nostrils are directed forward, small, simple, round, with the surrounding and bounding skin black, shining, quite bare, soft and constantly moist, the latter a certain indication of effective functioning. The lips are sparsely covered with short, buffy hairs and there are about fifteen tactile hairs on each. The lips are very thick and rubbery, barely noticeable externally, but flat and black within. The upper one is evenly rounded, the lower with two prominent internal tubercles just interior to the two front teeth, and fitting into small cavities in the roof of the mouth, close interiorly to the two upper anterior teeth.

Mentality

One occurrence presents an interesting comparison of the interplay of senses, and clearly indicates the level of mentality at which the lives of these mammals are maintained. Near the top of the enclosure tree was a three-quarter grown male asleep; seven feet below him was a mother sloth, from whom I had removed her month-old baby. I placed the infant sloth five feet away from the mother on a horizontal limb at the same height. At once the young sloth began calling, giving the identical plaintive whistle of the adults. Without answering, the mother showed at once that she heard, and her bullet head and marvellously versatile neck were turned and twisted in all directions. Many times she looked straight in the direction of her offspring climbing awkwardly along five feet away. But neither sight, hearing nor smell availed anything. Looking upward, against the sky she discovered the huddled ball of the large sloth, and at once climbed, as rapidly as her sense-bound mind and muscle-bound limbs would permit, straight up to the male sloth, reached out a tentative claw and sniffed with nose close against his fur. One second's test was sufficient, and she descended as rapidly, or as unslowly as she had climbed. The baby had seen his mother from the first and had struggled with all his little might to creep along

Fig. 9. Front view of the head of a month-old three-toed sloth. Photograph by John Tee-Van.

Fig. 10. Sloth in the heart of a cecropia tree, high above the Guiana jungle. It feeds almost exclusively on the leaves of this tree. Photograph by John Tee-Van.

the branch toward her. In spite of his chubby limbs which always kept getting in the way of one another, he made good progress, and was within two feet of the main trunk when his mother reached his level again. Her back was turned as she passed, but his whistles were ringing close to her ears, and his tiny claws caught at her fur as she went down, and yet she gave no heed, but reached the ground, and without hesitation, started out for the nearest edge of the jungle, looking up at each call of her baby and then hurrying on in the opposite direction. I went after her, picked her up by the middle of the back, the only safe place to hold a sloth,—and replanted her on the trunk. This time she was facing the young one, and at his first call, she reached out a tardy arm, he seized it and climbed down it to her body, and both were content. It is almost unimaginable to think of a mammal in full health, which, while actively seeking for its young, would have allowed an interval of five feet to separate her from it forever.

Hair and Skin

The logical placing, in this monograph, of a detailed account of the hair and skin of the sloth is difficult, for the reason that it is equally important from several wholly different points of view, physiological, symbiotical, and as being one of the most important fundamental explanations of the sloth's psychology and vital activities.

In this tropical land of superabundant animal life no outstanding characteristic is developed or maintained without a very deep and real cause, and this is equally true of the most specialized, recently evolved forms of life, as of interesting relics of the past, such as hoatzins and sloths. When we see birds of large size and conspicuous plumage, living exposed to a host of dangers, with weak flight and no defensive beak or talons, we may be certain that there is some compensating factor, hidden, but none the less powerfully operative ontogenetically and phylogenetically, day and night, at moments of safety and of extreme danger. In the case of the hoatzins this is odor,—a musky emanation apparently distilled in the course of the somatic analysis of the food, and deterring the attacks of the carnivores, eagles and serpents which, without such a repellent, could exterminate these helpless birds within a short time.

In sloths we find ten pacifistically defensive factors in operation, all of the utmost importance; first, the living, feeding and sleeping in

lofty, often small-branched trees, which would eliminate such heavy enemies as jaguars; second, the form, in repose like ant or termite nests or epiphytes, and in action with much of the animal outline obliterated by long hair, or unusually featured, jointed and graduated head, neck and limbs; third, the pigment mantle of lichens, moss and old leaves which is drawn over the hair. The coloration may be divided into three distinct sub-factors, *a*, the resemblance of both sexes during the dry season to dead vegetation or to the insect nests mentioned; *b*, the very appreciable greenish tinge imparted, during the rainy season, by the greatly increased brilliance of the symbiotic algae on the hairs; *c*, the brilliant mid-dorsal spot of the male, which, whatever it appears to represent, serves to break up the bodily form of that sex. Fourth, the pattern, which is of importance because of the variability, no two sloths being colored alike, the masculine orange spot, coming under this heading, also more valuable for not being an invariable indication of all individuals of this species; fifth, movement, or that most necessary corollary of protective coloration, the lack of it,—the animals being characterized by a large percentage of immobility, or very slow, deliberate movement, progress from branch to branch being made with absolute silence, noiselessly as a shadow. Sixth, the voice, again to speak rather Celtically, characterized by silence. When, very rarely, a sound is made, it is bird- or cicada-like, and very ventriloquial.

These might be called telegonous factors, or defensive phenomena acting at a distance, through space and the intermediate vibrations of light and sound. Or, to view them from another standpoint, all dependent for effective operation upon the imperfection of senses of the enemies.

The seventh is pose, the rolling up into a tight and firmly sustained ball, protecting the vital parts; eighth, the two dense coats of hair, ninth, the thick and very tough skin, and tenth, the greatly increased number and breadth of the ribs. These three are effective tactually, and of course only at closest range.

This bodily armor of hair, skin and ribs I consider the most important of all the defense of a sloth, which indeed, in the last analysis, would determine the continued existence of a degenerate race, such as these animals present today. It makes possible successful competition with a host of creatures, infinitely better provided with perceptual powers and defensive and offensive ability.

Three additional factors of defense form the Active or Dynamic

Defense of these animals, first, progress—an escape, slowly but in any direction, or a more balanced, secure advance through the branches than is possessed by any other arboreal mammal; second, claws used in swinging, scythe-like sweeps of the fore arm; third, powerfully muscled jaws armed with flat, crushing teeth which are used in biting. I have described these two last factors in detail elsewhere in this monograph.

These thirteen lines of defense may be charted thus:

PASSIVE DEFENSE		
A—Effective at a Distance	Distance operative	How Operative
1—HABITAT; Isolation in high trees	10–150 ft.	vision
2—FORM; Like termite nest or parasitic plant	10–150 ft.	vision
3—COLOR; Dry Season, like lichens, moss, dead leaves, bark	10–150 ft.	vision
Rainy Season, greenish like foliage	10–150 ft.	vision
4—PATTERN; Ruptive colored marks in male, irregular in female	10–150 ft.	vision
5—MOVEMENT; Motionless or very slow	10–150 ft.	vision
6—VOICE; Silent, or like bird or insect, also ventriloquial	10–150 ft.	hearing
B—Effective at Close Range		
7—POSE; Rolled into complete impenetrable ball, locked by claws		muscular resistance
8—HAIR; Two coats, very dense		hair resistance
9—SKIN; Thick and very tough		skin resistance
10—SKELETON; Ribs numerous and broad		bone resistance
ACTIVE DEFENSE		
11—PROGRESS; Climbs slowly but anywhere	any beyond touch	muscular action
12—CLAWS; Slashing hooks with fore arm claws	18 inches	muscular action
13—TEETH; Flat and crushing, used in biting	1 foot	muscular action

Examination of the pelage of the Three-toed Sloth shows two distinct coats, the long, coarse, yet silky hairs which bear the distinctive colors, grey, brown, black, white, yellow and orange of the adult, and the short, fine, wavy, silk-like body coat. The long hairs are flattened to an oval or almost a ribbon, presenting very distinctly broad and narrow sides. The longer, white hairs are more than twice as wide as they are deep, averaging .25 by .11 millimeter. In hairs from living individuals of the Three-toed Sloth there is no

trace of the longitudinal fluting mentioned by many writers as being common to all sloths and unique among Mammalia.

The surface is smooth, ivory-like, with occasional hints of the edges of the scales, which now and then near the tips show slightly. Sometimes, however, this segmentation of the cortex is pronounced and regular, so that the entire hair is marked with transverse cracks, which may be so wide that the hair looks like a string of closely strung beads. Among two or three hundred fresh hairs I found twelve which showed a decided longitudinal groove, and in each case there was no algae on the surface.

In the Two-toed Sloth the hairs are almost all distinctly fluted, there being usually four ridges and three grooves on each side. These are plainly visible under a 10 diameter lens, and a pile of mingled hairs from the two species can be sorted out at a glance. Even the arrangement of the algae is distinctive, its distribution in *Choloepus* being longitudinally along the grooves, and in *Bradypus* in short, lateral tongues or lines, especially marked in hairs which show distinct cortical segmentation. The soft under fur is round in section, never more than .05 of a millimeter in diameter, colorless, translucent, and quite free from all parasitic or other detritus. It is usually wavy.

The hair as a whole grows very closely together from small tufts, closely resembling the down of nestling birds. These are .2 to .6 of a millimeter apart, and each clump consists of six to twenty separate hairs. These may be all short, soft, under-fur hairs, or a single white or brown or grey hair of the long coat may spring from the heart of such a clump. I could find no long hairs arising alone. They seem always closely associated with the shorter coat. The relative average lengths of the short and long hairs are twenty-five and fifty millimeters, or 1 to 2. Between the eye and ear the hair is thirteen millimeters long, while its maximum length is on the nuchal cape, and on the upper arm, where it may reach one hundred millimeters.

I have casually mentioned the presence of an alga on the hairs of the sloth, and I have never found an adult animal without an abundance of this lowly plant on the long hairs of the pelage. When the sloth is perfectly dry the algae appear only as a dirty brown, generally-scattered pigment, which tones down the ivory whiteness of the lighter hairs. When the fur is wet, and especially after a few hours of soaking, the whole surface assumes a more or less green

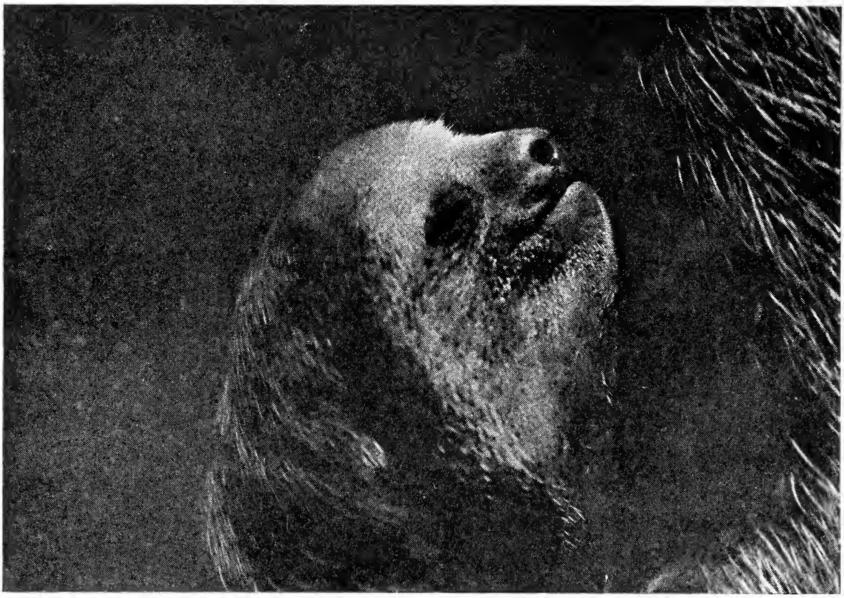


Fig. 11. Profile of the head of an adult female sloth. Photograph by William Beebe.

tinge, which in patches may appear of an intense green. We are at once reminded of the relationship between hydra and rotifers, and algae, but direct comparison is impossible: The symbiotic benefit derived by the sloth, while actually from the chlorophyll, is an added pigmental protection in place of interchange of respiratory elements. I have hung up a sloth among green leaves before and after dipping in the river, and it required no imagination to see a very appreciable difference in conspicuousness. This would be of value as additional concealment from enemies flying overhead, but hardly from those looking up and seeing the animal in silhouette.

The amount of algae seems independent of season, but more directly connected with the shedding of the fur. In one individual whose hairs were loose and apparently in full process of being shed, there was comparatively little green, but an abundance of dead algae.

The algae is equally abundant on the dark hairs, grey or black, and the white, the latter being sometimes almost covered. It is most conspicuous on a newly grown white hair, appearing as small, irregularly transverse patches, extending from a quarter to half across the surface. Under lower power they appear homogeneous,

but greater magnification resolves them into distinct pieces fitting each other in outline, but slightly separated. Each has a lighter green centre. The dead algae are of a light purple color and on most hairs are in excess. In the dry hair the apparent loss of green is due not only to actual dulling and clouding of the surface, but the edges of the minute fronds curl up slightly. A water film instantly causes the brilliant color to flash out. There is no trace of this algae on the young sloth up to about four months of age, and then only in tiny, isolated patches.

The direction of the hair on the entire surface is adapted to shedding rain when the animal is in the position of rest, which, as I have elsewhere described, is never normally upside-down. On the dorsal head and neck the elongated cape of long hair is parted in the middle; the direction elsewhere is, body down, upper arm up, fore arm, legs and tail down.

The skin of an advanced embryo, which I removed, was as tough as that of an average adult monkey, while the hide of a full-grown sloth is much thicker. The well-worn accounts of the toughness of the skin of the sloth is, therefore, strange to say, not over-estimated. On many parts of the body, the skin of an adult sloth is as much as 3.5 mm., or a full eighth of an inch thick, and tough and gristly as well. In addition to this, the under-fur is excessively dense, curly and thick, and forms a solid mat, as effective as sandbags on a trench parapet. A skinning knife becomes dull very quickly when used on sloths, and a pair of scissors often turns, as if cutting cartilage.

The multiplication and flatness of ribs of the sloths have frequently been instanced as adaptations to an inverted position, an osseous basket of sorts which serves to relieve the strain on the viscera. Disregarding the fact that less than ten per cent of the entire life of a sloth is spent upside down, it is interesting to compare its body with those of a typical monkey, and of a terrestrial mammal, such as an agouti:

	Agouti	Cebus	Sloth
Weight of animals	6.5	7	9.25 lbs.
Weight of abdominal viscera	1 lb. 10 oz.		3.5 lbs.
Length of intestines	16.5 feet		10 feet
Number of ribs	26	30	30
Width relative to the length	5%	4½%	11½%

This comparison does not sustain the idea of the necessity of increased provision for visceral suspension. On the other hand, when, as we have seen, the chief defenses of the animal are two thick coats of hair and an exceedingly thick and tough skin, we can readily appreciate the advantage of having a third line of defense in the shape of a lattice-work of close-set, hard bones. A direct comparison may be made with the little anteater, *Cyclopes didactylus didactylus* of this same region, whose ribs form an even tighter box of bone.

Teleologically, I should perhaps have introduced the subject of increased number of ribs with a discussion of the correspondingly abnormal number of dorso-lumbar vertebrae, but however that may be, it is at least an indirect factor of importance in the defensive congeries of this superlatively arboreal mammal, for by means of this vertebral flexibility the rolling into an absolute round ball is made possible. When the sloth spheres, the head and neck, both ends of the body and all four limbs, together with the upright branch to which it is clinging and the horizontal one upon which it is resting —all contribute to close the one vital weakness, the unprotected intracostal periphery of the body cavity.

Many a hawk of moderate size must strike in vain at the apparently soft furry body in the crotch of the tree, and I have hung up the fresh skin of one of these animals and fired a charge of shot at it at fifty feet distance, and had many of the shot flatten themselves just below the surface. The difficulty of killing a sloth is really four-fold, the dense pelage, the thick skin, the bony protection and the remarkably low physiological vitality, while even after actual death, the claws will often remain flexed, and thus suspend the body out of reach in apparently living resistance to gravitation.

Sloths live at such a low ebb, in a perpetual aestivation of sorts, that they outrage all the viability extremes of the other mammals, and approach closely the cold-blooded, defective heart-chambered reptiles. I have heard of a sloth living after forty minutes' immersion under water, and have myself seen one recover from a half-hour of complete submergence. I have known a sloth to act normally for a long time after it had received a wound which practically destroyed the heart, and their recovery after less severe wounds, and freedom from infection in lacerations is very remarkable. A sloth which I kept in captivity on a river-steamer apparently died, and showed no signs of life. I stuffed its mouth with cotton and placed it on ice in the ship's refrigerator, and next morning, after an hour's thawing in

the sun, preliminary to skinning, the animal began to show co-ordinated movements.

Enemies

To sum up, and to introduce the subject of enemies, the great natural timidity, the remarkable protective characters apparent in pattern, color, form and posture, and the ability to defend itself after a fashion in the last extremity, all point to a life surrounded by many potential dangers, and it is probable that more creatures than we know, attempt to kill these handicapped mammals. A direct comparison may be made between sloths and their unlike but undoubted relations, the armadillos, the possession of a protective epidermis. And while this is not carried to the extreme of the armored Dasypodians, yet it is a very real defense. The cringing from attack into an arboreal ball is another armadillo-like character, and few raptores except the mighty-taloned harpy eagle could successfully injure a sloth in such a position. This conventionally accepted hostile association of sloth and harpy eagle, in the rôle respectively of victim and assailant, has been quoted and requoted in almost every natural history and book of travel. I can verify a widely accepted fact as possessing a basis of fact, for I have shot an immature harpy eagle with wads of three-toed sloth hair in its stomach. On a heavy branch or near the ground, a jaguar would make short work of a sloth, rolled or unrolled, but an ocelot, while its claws would make grievous scratches, would have no easy matter to maintain its footing high up in a tree and at the same time dislodge the hold of the twelve strong claws. A man unaided cannot pull a sloth off a branch by direct force.

I can add the anaconda as a definite enemy, for I once found a sloth's skull among the few recognizable stomach contents of a large snake of this species which itself had met death in some unknown way, and was almost returned to its various elements. Again a red coati-mundi had bolted the unmistakable tongue and upper windpipe, but this was undoubtedly a relic of scavenging after a harpy's feast or that of some other more probable victor. The whole lower jaw and manus of a very small three-toed sloth was found among motmot's feathers in the stomach of a margay cat, while the animal itself had a terrific gash across one side of the face, perhaps given by the mother sloth while the young animal was being attacked. This carnivore, while no larger than an ocelot, is much more arboreal, and

as I have found the remains of a cebus monkey in its food, I can well believe it capable, under favorable conditions, of tearing a baby sloth from its mother.

From more subtle enemies such as parasites, sloths seem remarkably free internally, as vegetarians usually are, and externally, probably as a direct result of the dermal and epidermal barriers. I have never known either young or old to be afflicted with bots, but I have seen them extremely annoyed by the large red bees, *Xylocopa fimbriata,* trying to alight on the nostrils, attracted by the moisture on the surface of the tissues.

The only true parasite I have observed on these animals is a species of large and ornate tick. This creature frequently comes to the tips of the hairs and crawls about in full view. One mother sloth which I kept for a long time in captivity had six of these acarids on her body, and when her six-weeks-old infant died, I found four of the ticks in its fur. The ticks are 8 by 5 mm. in length, pear-shaped, flat, and of a rich russet brown, variegated on the back with golden yellow, dotted with brown. There is a swollen, rounded rim extending clear around the body, thickest along the posterior half, where it is divided into about a dozen radiating segments.

These three animals, a mammal, a bird, and a reptile, sum up my knowledge of the sloth's enemies. The fact that the sloth is asleep and motionless on a lofty perch during the night, makes it less likely to fall a frequent victim to prowling jaguars, while its diurnal habits and usual exposure skyward would make it likely that all the hawk eagles which pass must have opportunities of perceiving and attacking them.

Tough and thick as the skin is in general, there are spots which are vulnerable to tiny annoyers. This is easily seen when a splintered branch of cecropia is given a sloth, out of the nodes of which a swarm of tiny Azteca ants are pouring. Soon after feeding is begun, the sloths show signs of restlessness and sometimes the host of little stinging demons actually drives the sloths away. The latter then suspend themselves by their hind claws and begin a frantic but wholly ineffectual scratching of the whole of their heads and bodies, their claws ploughing wildly through the fur in all directions. The ants are certainly able to force their way down through the dense inner fur and at certain points to penetrate with their diminutive stings to nerves in the skin.

Neither thick skin nor dense coat of hair serves to protect the

sloth from the full glare of the sun, and a sloth given no shade will die within four days, as I found to my regret when I was a greenhorn in knowledge of the ways of sloths. Once when I had no facility for a sloth to climb about, I confined an animal in a box and in three days its feet were so raw from the unaccustomed pressure, that it took as many weeks of care to get the sloth into condition to be photographed.

Friends

The innocuous character of the sloth is apparently a matter of common knowledge among birds and other arboreal creatures, for they show absolutely no fear of them. I have seen small birds feeding unconcernedly within five or six feet, and flycatchers and manakins will often come close to have a good look at the inverted creatures, as if surprised as much as we are. Aside from this tolerance, the sloth itself is too self-centered, too subreptilian in mentality to be able to conceive any relationship with its tropical arboreal neighbors other than patiently to await their approach to see whether they themselves are to be ignored or doomed.

Inter-Communication

The native name of *ai* for the Three-toed Sloth is onomatopoetic, but no syllables or vowels will serve to represent their strange utterance. They are unnecessary, for it can be imitated almost exactly by a simple whistle. I have never heard it from the adult except when the animal thinks itself in extreme danger. Sometimes when I come suddenly up to one of my sloths and stroke it, the cry is given, or when I unhook it from a branch, and once when I tied one up in a sack so it could have its portrait painted, it called continuously. The young sloth also calls when separated from its parent, and when placed by itself on a branch, or on the ground, continues to call until rescued. The mother never answers during her search for her offspring. The young are easily reassured, and the moment they secure a firm grip on any satisfactory surface, hair, clothing or flesh, they cease crying.

There is little difference in tone or timbre of the cry of a new born sloth or fully adult sloths of either sex. It is a plaintive, shrill, penetrating whistle, beginning on D# above middle C and holding true for several seconds.

My attention was attracted one afternoon to a moderately tall tree by the cry of a sloth on it, the call being given five times without any apparent reason. Although I have seen these animals courting

in captivity, and enraged, advancing to their pitiful attack, yet neither of these emotions, nor the loss of their young, ever moved them to utter a sound. Except in the very young animal the cry is given through the nostrils with the mouth closed, yet when heard near at hand, it is almost painful in its shrillness. Its duration is never more than two or three seconds, and the farthest I have ever been able to hear it is two hundred feet. It is very similar to the ordinary call-note of the small-billed kiskadee flycatcher, *Pitangus lictor* (Licht.), and I have been deceived many times and gone to the sloth enclosure to see what was the matter when it was only one of these birds calling from a neighboring tree. Of still greater interest is the reaction of sloths themselves to this bird note. Three separate times I have seen one, five and two sloths respectively, raise their heads and gaze intently in the general direction of the flycatcher, very evidently deceived by the resemblance.

Taking into consideration the extreme dullness of the other senses of the sloth, I believe that the voice is of equal or greater importance in enabling these animals to find one another in the mating season. I have had, however, no first-hand evidence of this. Vocally, the sloth occupies a very low place among mammals, both in physiological specialization and in variety of expressed emotions. Also it is interesting to observe that the young shows no improvement in the matter of voice, so its character is not due to ontogenetic degeneration.

The cry of a sloth is very high in the scale, dropping slightly at the end, and is not far from the upper limit of human whistling. A most interesting thing is the way their hearing is exactly attuned to this note. I once placed two mother sloths in a cage, and took away their offspring. Going sixty feet away I gave the call. Slowly but surely both heads turned in my direction and a male high up on his tree also turned at the same instant.

This tone was upper D#. I then waited a while and gave upper C, then E, then upper B with no result whatever. Again I whistled D# and the reaction was as instantaneous as a sloth can achieve. With difficulty I whistled higher, then began at C and whistled a sudden rising scale as high as possible, arousing no attention. I repeated this on different days, with various individuals and found that while unattached sloths paid no attention to a note above or below, an anxious mother sometimes looked around at half a note below. But usually even D had no effect, while D# aroused all

the interest which their poor, dull minds could bring to bear. When one is attacked by another sloth the victim rarely utters this absurd tin whistle of a cry. It is their only vocal expression of emotion.

Food and Feeding

I have made a great many tests with plants of various families and have found no food acceptable to the three-toed sloth except cecropia or pump-wood, *Cecropia palmata*, and wild plum, *Spondias lutea* Linné. The latter is refused by some individuals, and when the two are offered, the plum is never touched. The leaves only, of the plum are eaten, but besides the cecropia leaves, the leaf buds, terminal shoots, petioles, and the main stem itself, where it is still green, are devoured with relish.

When I put a large cecropia shoot in the sloths' enclosure the method of feeding of different individuals in various months or years is exactly the same. The sloth, if asleep, is awakened by the swish of the leaves, and slowly unwrapping itself, climbs down. When near, it reaches out a long forearm and hooks in a leaf, drawing it around until the tip is within reach of the slit-like mouth. Or if all the limbs are in use, the head is stretched out and twisted until the edge of the leaf is encountered. The chewing is continuous, one or occasionally two bites every second, and as the leaf substance is ingested, the head is shifted laterally. Thus the entire lobe is gradually devoured by a series of lateral swings. Unless disturbed, there is no break, and the swallowing is wholly incidental, there being not the slightest indication of it in the regular rhythm of chewing. There is no lateral movement of the jaws, the bite being direct, and the separated leaf tissue removed by successive forward and back movements of the tongue.

Considering the size of these animals, the amount of food they consume is surprisingly small. I once tested the weight of fodder taken by a young fawn of *Mazama nemorivaga* (F. Cuvier), and although the weight of the deer was exactly that of a large Three-toed Sloth, yet the amount of food consumed was seven times as great. Some sloths feed only every other day, and now and then a three-toed individual will be captured which refuses all food and starves to death after two or three months' fast. This is very seldom the case in their native country, but this species will not adapt itself to any strange diet, and so is wholly unsuited for captivity in northern zoological parks. The two-toed, on the contrary, feeds readily on

Fig. 12. Mother and young three-toed sloth, the parent in full movement. Photograph by William Beebe.

Fig. 13. Mother and young two-toed sloth. Observe shorter fore-limbs and longer hair. Photograph by Elwin R. Sanborn.

fruit and vegetables, especially bananas, and bread and milk, and has lived for years in the London and New York Zoos. I have never seen a sloth drink, and it is probable that it obtains sufficient moisture in the tissues of the leaves. Morning and afternoon are the regular times of feeding, although on cloudy days I have seen them eating at midday, and occasionally late at night in full moonlight.

The lips are flush with the outside skin, and flat on their apposed surfaces. They are thick and leathery, and the irregularly disposed, low tubercles, which are scattered over them, together with the two larger projections on the center of the lower lip all aid in holding fast the leaf while it is being chewed off. The tongue is pale flesh color, large, thick and soft, reaching quite to the lower lip, filling the whole space between the two rows of mandibular teeth, and extending well in front of the anterior teeth which are 8 mm. apart. The upper surface of the tongue is tumid, with three deep, longitudinal furrows and several, shallow, obliquely-transverse ones. The entire surface is densely covered with minute, transparent, sharp, backward-directed spines, averaging twenty-five to a square millimeter, and extending back almost to the level of the angle of the lower jaw. The tongue measures about 35 by 11 mm., giving about ten thousand spines in all. The organ is thus a most efficient ingesting apparatus, and explains the possibility of continuous, uninterrupted chewing, while the bitten off portions are carried back and down by the tongue.

Not only the inner lining of the lips, but the circumdental tissue, the roof of the mouth, and assymmetrical lingual blotches are jet black. The palate is roughened, and covered with a number of coarse, irregular, raised ridges, short, and more or less transversely oblique. In the upper jaw are five teeth on each side, four isolated, rounded, molar-like teeth, hollowed in the center, and a fifth anterior pair, peg-like and solid with the upper surface worn obliquely backward. These are wide apart medianly. In front lies the semi-loose, cartilaginous premaxillary, toothless, with only a complexly folded bit of black, terminal, palatal lining between it and the mouth. In the lower jaw are only four teeth on each side, all of the concave rounded type. The chin and lower jaw are remarkably deep, affording excellent attachment for strong chewing muscles. The depth is equal to the distance from the line of the mouth to above the eye.

The hyoid is intimately connected with the ear, and is separated only with difficulty.

Digestion, like the other physiological and the mental processes, is slow, much more so than in other herbivorous mammals. The mouth has no great gaping power, and is slit-like, well adapted to receiving and chopping off the flat surfaces of leaves. The animal has much more trouble when it begins to feed on the good-sized, round stems. The oesophagus is small in calibre and short. The stomach is very large, about 120 by 100 mm., and very complex. In the large anterior compartment the leaves form a finely comminuted, pale green, moist mass, while in the enormous coecal diverticulum, they are still green, but almost dry, while in the intestine the ingested material consists of blackened, dry fibre. The excrement is in the form of small oval pellets, about 10 by 5 mm., and, at least after a diet of cecropia leaves, is composed of matted, black, cellulose fibres.

The liver is relatively small, high up on the right side, closely applied to the dorsum and to the diaphragm, 75 by 55 mm. and 20 thick. The lobes are closely united.

The large intestine is 80 mm. in length and merges gradually into the small intestine. This has a total length of 1925 mm. or 6 feet, 4 inches, and is of rather small, even calibre throughout. The bladder is very large, sometimes 120 mm. in diameter.

Roosts

Sloths sleep at least twice as much as any other mammal with which I am acquainted. One nearly grown male in good color and health, eating regularly a full quota of food, lived for months just outside the laboratory. I timed his activities for a week, occasionally looking, or going out at night, and keeping a close watch on him during the day. His existence on earth during that period of 168 hours was divided into 11 hours of feeding, 18 of aimless climbing about, 10 of resting and looking about or lazily scratching, and 129 hours of sleep, an average of 18½ hours each day. What an ideal life for some people!

Sloths have favorite sleeping places to which they return regularly. I have seen this occur five times in succession in the case of a sloth at liberty, and for many weeks in animals in confinement. No attempt at a nest or shelter is made, and no protection sought against rain or sun other than the jungle foliage.

I have never seen a sloth sleeping upside down, except in a cage

where there was nothing but a horizontal bar to which to cling. The first desideratum is a vertical branch or stem. Upon this the sloth will settle to rest by taking a firm grip with all four feet, letting its limbs hang obliquely downward, turning the head and neck forward and in between the front legs, and setting the tail firmly against the side or front of the support. When given opportunity to choose, all sloths adopt identical sleeping poses. They seat themselves upon a sloping or horizontal branch, gripping with both feet the upright stem to which it is joined, head curled down upon the chest in front, and both forearms curved around head and body. To such a roost and pose they return on every possible excuse. I have had a sloth wholly occupied in trying to injure me with languid hooks and still more desultory bites, when at the first drop of rain, all wrath was forgotten, and he climbed without hesitation to his regular roost. In heavy wind, as well as after feeding, they retire to it at once, and for the night, early every afternoon, while they leave it reluctantly, long after every other diurnal bird and mammal, including ourselves, are abroad and doing.

The roost I have described is the only home a sloth can be said to have. Once a pile of sign on the ground indicated a long stay at such a place. I cut down the tree, and found deep grooves where the claws had cut in during sleep. Cecropia trees were abundant close by and it is probable that this particular crotch was occupied for at least three weeks. The cecropia is the dining room of the sloth, the mid-height jungle is his estate, while his highway lies beneath the limbs. No wonder it has survived from ancient times without need for keenness of sense; no other creature in the world would dispute either food, paths or sleeping place.

Courtship

I have watched two courtships, one of an immature male and the other of an animal of full size and color. Both were alike in their absolute directness and simplicity. The male climbed up to the female and when within reach, stretched out an arm and attempted to pull her down, exactly as he would haul in a cecropia leaf. In the first instance where the female had a month old baby clinging to her fur, she lunged leisurely with full force at the disturber of her peace. The other female simply mounted higher, and when she could ascend no more, she climbed down and across her suitor, leaving him stranded on the lofty branch looking vaguely about, and reaching

Fig. 14. Three-toed sloth; embryo within a few days of birth. Photograph by John Tee-Van.

out in vain toward a big green iguana lizard on the next limb in mistake for the fair companion of his tree. This unemotional pursuit continued for an hour, when he gave up for good and went to sleep. Throughout it all, although he was as enthusiastic as a sloth could be, not a sound was uttered, not a feature altered its stolid repose,—the dull eyes only blinked slowly and the head moved mechanically, striving to pierce the opaque veil which ever hangs between its brain and the sights, sounds and smells of this tropical world. If the orange ear-spots, and the brilliant mid-dorsal sun painted upon the fur of the male were ever of any value in courtship, it was in ages long past when the ancestors of sloths, contemporaries of their giant relations the Mylodons, had better eyesight to escape from sabre-toothed tigers, than there is need for today.

The courtships, like the restlessness of the migrating males, take place in the tropical spring, in March and April, before the beginning of the long rains, and the births of ten young of which I have data, were distributed as follows, July 2, August 7, and September 1. I have reliable reports of very young sloths in May and October, so there may be considerable latitude in the extreme of the breeding period.

To sum up the general phenomena of this phase, the male makes no use of his bright colors, or any other secondary sexual character, and his courtship is unemotional, direct and brief. I have no shred of evidence that he exhibits any interest whatever in the young, nor in fact, that he remains in the company of the female for more than a few hours.

Young

Only a single young sloth is born at a time, and although I have made many inquiries in various countries I have never heard of an exception. As a rule they are born at the beginning of the long dry season, late July, August and September, with the focus of births about August 1st. Sloths dislike rain and their hair soon becomes drenched through in a heavy downpour. They often give up feeding rather than climb about in a severe rain, and a mother sloth will go without food two days rather than uncurl and expose a young animal to the wet. This is probably a factor in the season of births, coming at the beginning of four months of least rainfall.

I have never had a sloth born in captivity but I have had them a week old, and have taken an embryo within a week of birth. When this latter was washed and dried, except for the dulness of its eyes, it could not be told from a one or two-week post-natal individual.

Fig. 15. The same embryo as in Fig. 14, dried and relaxed to show perfection of development at this stage. Photograph by John Tee-Van.

There is considerable difference in relative dimensions among young sloths, and the individual variation in color and pattern is as great as in the adult.

The first coat of hair of the young sloth is so well-developed in the late embryo, that, as I have said, it cannot be distinguished from that of an animal many days old. The hairs are very soft and fine, even softer than in the adult. As to length, on the top of the head the length is 23 mm, at the elbow 30, on the midbreast 26, on the knee 23, and on the mid-back 30 mm.

With the exception of the nostrils, the sub-nasal lip area and a narrow line down the sole, from claw base to heel, every part of body and limbs is clothed densely with hair. The pelage, as a whole, differs from that of the adult in the greater quality of length of the two coats. Where the longer coat is 30 mm., the under fur is 25 mm. This accounts for the greater softness of the juvenile covering. In the six-weeks sloth, a radical molt is perceptible. The whole body shows active growth of a multitude of the thicker, longer hairs, averaging at this age, only a third in length of the functioning natal coat. This change is especially noticeable on the parts which have had the most wear, such as the palms and the inner side of the fore-arms. Here there is a solid coat of this new fur, conspicuous by reason of its white and pointed tips.

The most marked differences between adult sloths of opposite sexes are the brilliantly colored aural and mid-dorsal spots in the male, and the greater development of the mat of hair on the head and neck of the female. The males are also considerably smaller than the females. The young male sloths show none of the external pigmental differences, but are wholly like the female in pattern and pelage. Even at birth, however, the males average smaller. The dominance of the under, wavy fur gives to the long hair of the head and neck a more disturbed, frowzy appearance than the sleek, smooth parted mop of the adults.

The individual hairs are, if anything, flatter than in the adult, but average smaller in calibre. They are, as a whole, of a uniform drab color, with the light dorsal patches composed of hairs abruptly white, with enamelled surface, showing no trace of algae until after the second month. There is no hint, not only of longitudinal fluting or grooving, but even of transverse segmentation.

The normal position of the infant after birth is flat upon the mother's ventral body, with limbs wide-spread sideways, gripping

her long hair on the sides of the body. From this point of vantage, by a turn and twist of his mobile neck, he can reach either breast, the glands being placed high up and well to each side of the middle line. He can also turn his head directly backward and look at the scenery, upward, if his mother is climbing along a horizontal limb, or around at the horizon, when she is sitting upright in the resting or sleeping pose. Until a month or more old the young one seldom if ever leaves this refuge under the parent's body, and even after that I have never seen him sprawled for any length of time in a corresponding position on her back, as is so frequently described in the casual observations of travellers.

The strength of grip of baby sloths is unbelievably strong and whenever I have occasion to pull one off quickly, four large tufts of hair come with the claws, showing how tightly he grips the fur.

No matter whether we are interested in sloths from embryological, ontogenetical, or physiological points of view, if we are human, we cannot escape the charm of these little fellows. Next to young bear cubs, which they resemble in many ways, they are the most amusing and delightful of pets. They show no fear, and cease their plaintive wails as soon as they can get all four feet fixed in one's clothing. The vacant expression, which in the adult is one almost of idiocy, becomes infantile and quite suitable to these tumbling little bundles of grey and white fur. They take milk from a medicine dropper readily, and after a few weeks will contentedly munch leaves from the hand.

On the sixth or seventh day the young sloth begins a series of gymnastics, by freeing one or both his front limbs and leaning backward, sometimes completely reversed, or also stretching far to one side. This phase of activity reflects much of the adult movement, which corresponds to the progress of a legless man. The hind legs are passive followers of the front ones, and almost never venture to lead or reach out for a grip of their own. For a few days the young animal revolves about the grip of his hind legs, extending into the most amazing attitudes, and often hanging with his head dangling far out between the mother's knees and body. After courage has come to clamber about he deserts this hydra or leech-like attached movement, and for a few weeks, becomes much more of a balanced quadruped than his parent, and at this time the limbs are correspondingly different in proportion, being more equal in length. The whole mother now becomes his tramping ground, and when she is

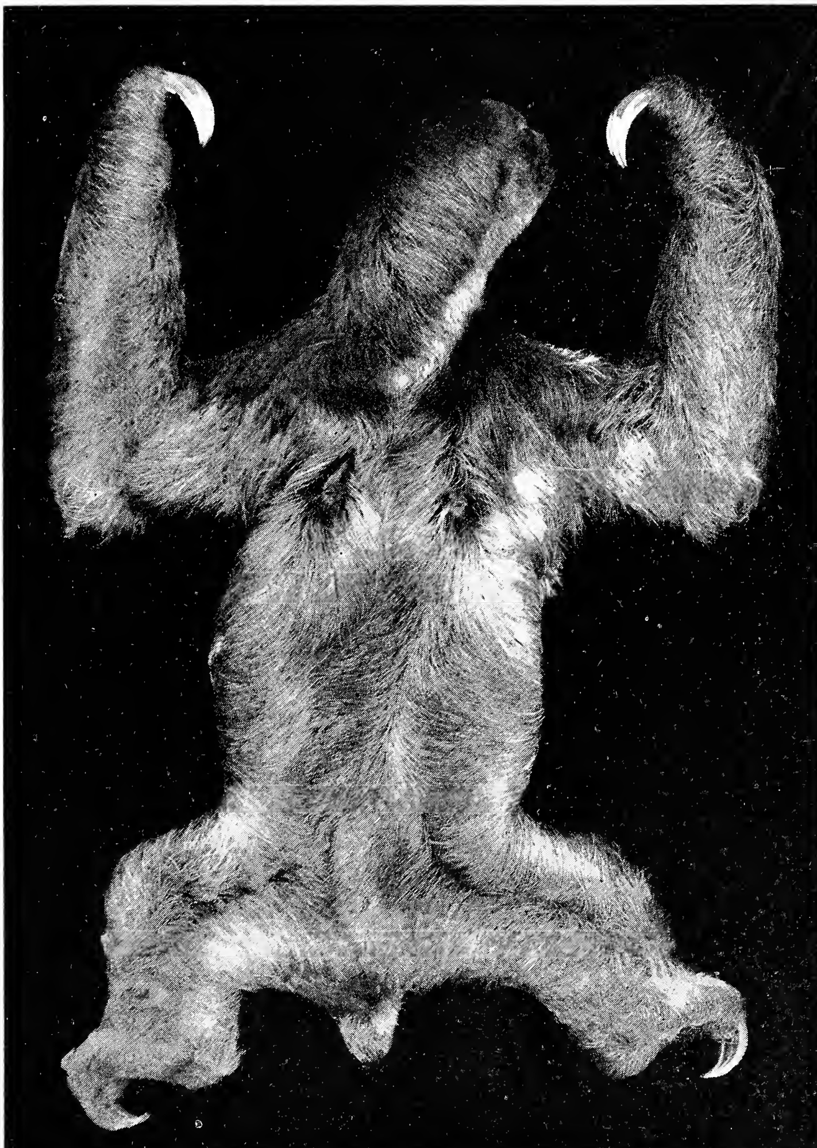


Fig. 16. Adult female three-toed sloth. Observe lichen-like marks, well developed tail and rain-shedding slant of hair. Photograph by John Tee-Van.

quiet, he climbs about, sometimes over her head and face, while she suffers patiently his sharp little claws on her eyes and nose. He fumbles his way out to the top of an outstretched arm or leg, and when the parent is weary of his activity, she sweeps him back with one circle of her arm. Nothing could be safer than his normal position, for when she rolls up, with head down and forearms crossed over all, the baby is in the very heart of the ball which she forms, and she can swing with one or both claws and forearms without exposing him to danger.

After she has fed heartily and especially if the day is warm and rainless, she often lies on her back along a branch both feet gripping tightly, forearms partly raised and spread out, with head and neck blocking up the anterior gap. In this living cradle, hollow and lined with the softest fur, the infant sloth approaches play as nearly as these solemnly dull creatures can. He seizes a tuft of hair on her neck and makes comic little swings at her fur, with first one arm, then the other. In doing this he often actually stands up for a minute, holding on with all four feet, and with hind legs very much spread and unsteady. It is only a temporary and passing feat, but the old sloth cannot do it even for a moment, and we have in it a hint of the long past ages when sloths could shamble upright along level ground.

The senses of the young sloth are keener than those of his mother, and he perceives my approach before she does. If the animals are newly caught, his reaction is to lean forward, and look curiously at this strange being, who does not walk upside down along a branch. She, on the contrary, rolls up, closes her eyes, and enfolds him in the depths of her body and limbs. After several weeks in captivity the parent pays little attention to my presence, and allows me to play with the youngster, showing her usual stolidity and lack of interest. His sense of smell is less acute than hers, but his hearing is much better. I found it difficult to get a full-timed photograph at first because of the instantaneous reaction of the young one, his whole body quivering and giving a sudden jump at the noise of the shutter. The sloth cry, too, will attract his attention at greater distance than it will one of the adults.

About the third week the young sloth begins to claw at the face and mouth of the mother. For some time I could make nothing of this, as it was too persistent and studied for play. I watched, and one morning, after five minutes of this teasing, with the infant open-

ing its small jaws and licking the mother's mouth with its little red tongue, I saw a glint of green, and realized that the young sloth was weaning itself from milk to predigested cecropia leaves. I am certain that the mother had not fed since the afternoon before, as she had not changed her position near the top of the branch, and the leaves given her at dusk had not been touched. Later I verified the fact that unless she held the chewed leaves in her mouth for fourteen hours, which is absurd, there must be actual regurgitation. The digestive processes are so slow that the food would still be available from the anterior part of the stomach after such an interval of time. I secured a bit of this vegetable pap and found it of the same consistency and alkalinity as the contents of the organ mentioned in recently killed sloths.

Young sloths, according to my observations, begin eating tender leaves and even chewing at stalks when five weeks old, and thereafter for a month or more the pampered youngster may choose between a milk diet, predigested food or fresh green cecropia leaves.

When about a month old the baby sloth leaves its mother for the first time, in one instance clinging to a huge cecropia leaf which it was mumbling with but slight success. When it reached around and found no fur at hand, it raised a wail which drew the attention of the mother at once. Still clinging to her perch, she stretched out a fore limb to an unbelievable distance, and gently hooked the great claws around the huddled infant, which at once climbed hastily up the long bridge and tumbled headlong into its natal hollow.

A young sloth never flinches from an attempt to free it from its mother's fur. It hangs on for dear life, but when the last clawful of hair comes away, it rolls around in one's hand and reaches hopefully for some new grip on clothing or flesh. It has no knowledge of rolling up into a ball or of hiding its head on its chest. It ceases calling after a few seconds and only worries if it has not twelve clawfuls of something. More than once when playing with a baby sloth it has drawn back and struck out right manfully at me.

Even week-old youngsters are painful to handle incautiously, for their grip on flesh is a pinch between claw tips and sole and the claws are slender and very sharp. The whole grip is unlike that of the adult, and is fitted for gripping a small tuft of hairs rather than a branch. When separated at an early age and forced to fend for themselves on a branch they are extremely unhappy and make very poor progress. The effort is constantly to put the whole arm on the

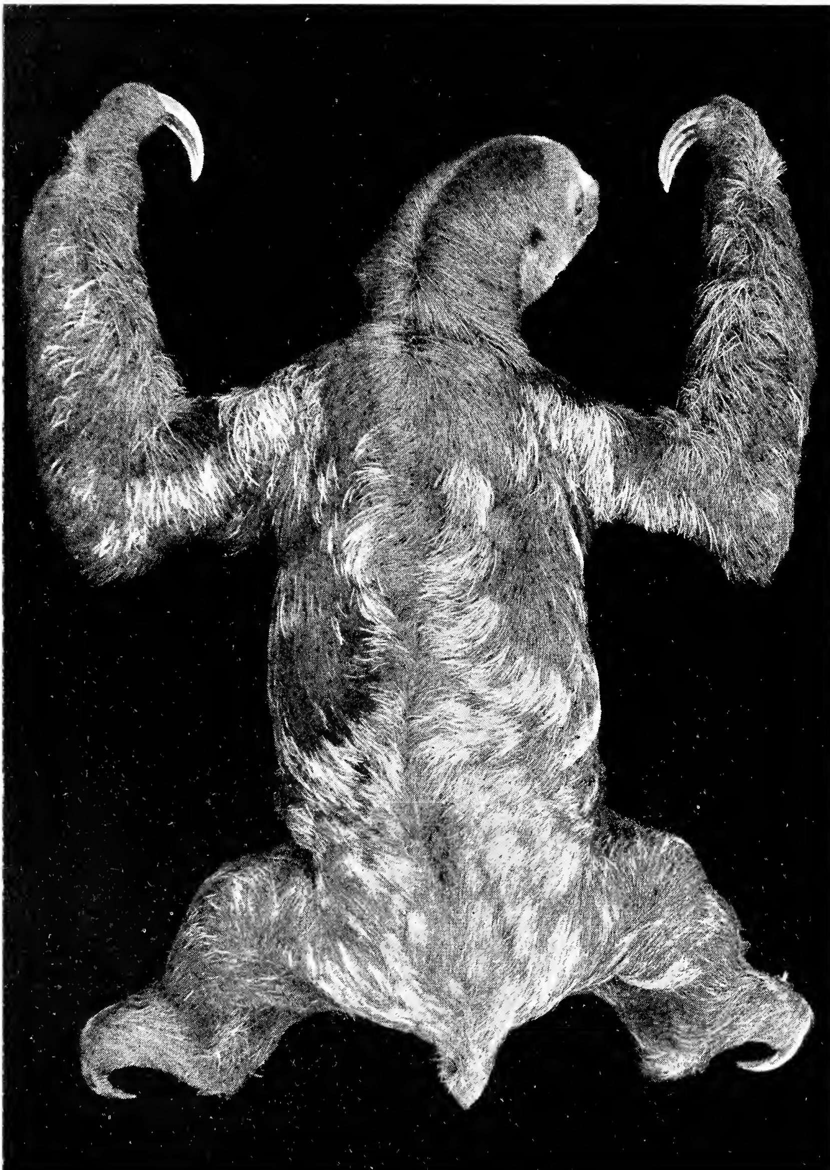


Fig. 17. Same as Fig. 16, lower view. Photograph by John Tee-Van.

branch and get on top. The inverted position is certainly not so casual a matter to the young as to the old sloths. They have difficulty in not stepping on their own claws, and when once a baby sloth has secured a grip on the hair of his own arm or body, he lets go of the branch with perfect confidence that hair is a better support than wood.

On the ground young sloths are quite helpless, and roll and tumble about in one spot without ever getting anywhere. This would seem to be a contradiction of the unusual quadrupedal ability which they exhibit on the body of the mother. But as a matter of fact the facility which adult sloths exhibit in getting over the ground is due to their complete divorcement from ordinary quadrupedal structure. When they were less specialized for arboreal life they progressed on the ground in an entirely different manner. This leaves the young hopeless on the ground, for while any remaining atavistic instincts or structural memories make for gathering their limbs under them, their proximity to adult sloth morphological conditions negatives any such accomplishment. One difficulty is purely a juvenile adaptation, the difference in the grip from that of the adults, for the young animals seem unable to stretch the claws straight out, having no use for such flexion in their progress about the mother's body, while this hooking of the claws in the ground is the most effective factor in the old sloth's terrestrial progression. But the principal reason is what we might call their positive pelagetropism. The moment one of their claws touches their own body, they seize the hair and hold on through all the subsequent efforts at progress on the ground The tail is a favorite point of seizure, and when one hand is gripping this organ and the other is stretched around the body holding tight to the leg on the opposite side, the little creature might be shackled and bound for all the use his limbs are to him; his small face grovels in the dirt but it never occurs to him that he might better his condition by letting go of himself.

Even in these comically abortive efforts we perceive an interesting corollary with the limbs of the adult, since only the fore legs are used to feel about and seize upon objects, while the short, stubby hind limbs stick straight out absurdly on each side of the body like a badly made doll, and function only in furnishing occasional anchorage for the forearms. The tail comes into use in helping to turn the young sloth over when on its back, functioning exactly like the hind legs of a scarab beetle in the same predicament. The tail twists

	BRADYPUS—Three-toed Sloth							*Choloepus* Adult 2-toed Sloth	*Choloepus* Adult Male	*Alouatta* 3 Weeks Old	*Alouatta* Adult Female	*Cebus* ¾ Grown Male	*Pithecia* Adult
	Late Embryo	2 Weeks Old	4 Weeks Old	½ Grown Male	¾ Grown Male	Adult Female	Large Adult Female						
Weight			310 grms.		2040 grms. 4½ lbs.		9¼ lbs.	8 lbs.	9½ lbs.		12 lbs.	7 lbs.	2¾ lbs.
Length, head and neck		85	89	150	165	175	200	165	165	62	84		70
" body		114			265		390	505	470				314
" tail	27	35	47	50	57	70	85			270	620	450	395
Diameter tail, half-way		20	20	20	21		27			11	15		9
Sitting height		190	200	420	380	500	500	470		190	480	390	330
Bimammillary diameter				70	90	72	73	43		46	100	60	
Mammary glands from arm-pit				32	38	55	58	26			17		
Chest, transverse diameter	44	44	43	110	100	100	125	100	90	70	110	85	72
" sagittal "		40	41	94	90	87	225	95	85	52	112	80	66
" circumference		130	135	290	270	290	320	280	300	160	310	260	215
Arms and claws, total length		162	164	405		455	480	450	430	160	370		245
Arm-pit to claw tips	123	140	150		330				430				230
Upper arm, length	51	60	65	160	140	182	190	160	175	63	152	120	93
Fore arm, "	54	59	62	155	134	176	190	180	200	64	146	125	97
Hand, length	39	43	39	76	73	79	74	103	105	60	105	82	74
" breadth		12	13	26	20	27	26	24	20	19	28	37	21
Hand claws, length	17	20	18	47	42	59	60	54	50	5.5	10		7.5
Legs and claws, total length		120	130	265		295	315	400	400	175	400		340
Thigh to claw tips	83	100	108		200								320
Thigh, length	37	39	43	100	86	112	117	138	156	63	170	145	130
Lower leg, length	33	40	45	96	86	105	100	160	156	63	150	140	138
Tibiale to sole		50	50	115	100	126	127	177	175	77	166	155	144
Foot, length	39	47	48	93	68	101	105	110	110	73	131	130	113
Foot claws, length	17	19	20	35	33	49	53	44	48	5	8		8.5
Foot, breadth		18	18	27	21	32	27	24	25	17	41	40	25
Head, total height		34	37	54	60	57	62	76	75	75	97	88	60
Ear to ear, transverse arc		40	50	85	100	80	100	195	140	70	90		80
Auricular height of head		17	17	24	22	27	36	40	40	25	21	25	17
Occipital to forehead		40	42	63	61	70	73	90	90	62	80		57
" " lips	47	51	53	78	77	90	88	115	120	79	128	101	80
Ear, height				10		10	9	21	28	32	38	41	31
" breadth				8		7	10	23	33	27	20	27	23
Interocular	19.5	19	16.5	30	27	31	30	47	45	12	19	11	9
Eye, diameter	5.5	6	7.5	9	8	10	11	12.5	12	13	14	14	11.5
" divergence		23°	24°		25°		25°	34°			4°		9°
Internasal		2.5	2.4	4	4	4	4	12.5	11	5	10	13	17
Narial diameter		2	1.8	3	3	4	4	5.3	7	4.5	7		5
Mouth, width		19	23	32	31	35	39	47	42	24	36	33	24
Nasals above mouth		2.5	3.3	5	5	7	6	11	11	5.5	11		3.5
Eye to ear		16	22.5	31	34	31	42	52	55	30	49		31
" " nares		10	11	17	14	18	16	31	33	11	25	23	17
Adpressed arm (minus claws)		20 mm. beyond tail	Half-way to tail tip	27 mm. beyond tail-tip	Roof of tail	To tail tip	Half-way down tail	80 mm. beyond body	To end of body	20 mm. beyond root of tail	To thigh, 50 mm. short of tail		10 mm. beyond root of tail

about strongly in every direction, and I found that, as far as strength went, it was quite sufficient to support the entire animal, when it was turned up over the back. This organ is surprisingly muscular, and as in the adult in motion, is never quiet, pushing and feeling about quite as much as the limbs. When the young sloth is lying quietly upon the mother's fur, the tail is often slowly wagging from side to side. It is relatively twice as long in the young as in the old animals.

When, on the ground, the baby sloth succeeds in sitting up for a moment, and reaches up toward your hand with both its small arms, and utters its appealing wail, it requires all the abstract, hardened desire for more knowledge of its activities to keep from restoring it at once to its mother. At such a time its resemblance to a bear cub is most striking.

The moment a baby sloth dies and slips from its grip on the mother's fur to the ground, it ceases to exist for her. If it had called she would have climbed down and hooked a claw around it, but simply dropping silently means no more than as if an entangled bur had fallen from her coat. I have watched such a sloth carefully and have never seen any search of her own body or the surrounding branches, or a moment's distraction from sleep or food. An imitation of the cry of the young will draw her attention, but if not repeated she forgets it at once.

Anatomy

Notes on the Anatomy of a Four-Weeks-Old Male Sloth

Immediately after death I made the following brief notes on the anatomy of a male sloth, about a month old:

Diameter of eyeball 8 mm.

Weight of skin 75 grams; skinned body 235; total weight 310 grams.

Tongue measures 23 by 10 mm. One square millimeter of the surface contains seventy-two teeth, making a total of lingual teeth of about seventeen thousand five hundred.

There are eight teeth in each jaw; the two anterior upper teeth just breaking through, not yet functional.

The heart measures 21 by 44 mm.

The lungs are large for the size of the animal, 31 mm. wide, by 13 thick, 25 long anteriorly and 44 mm. posteriorly.

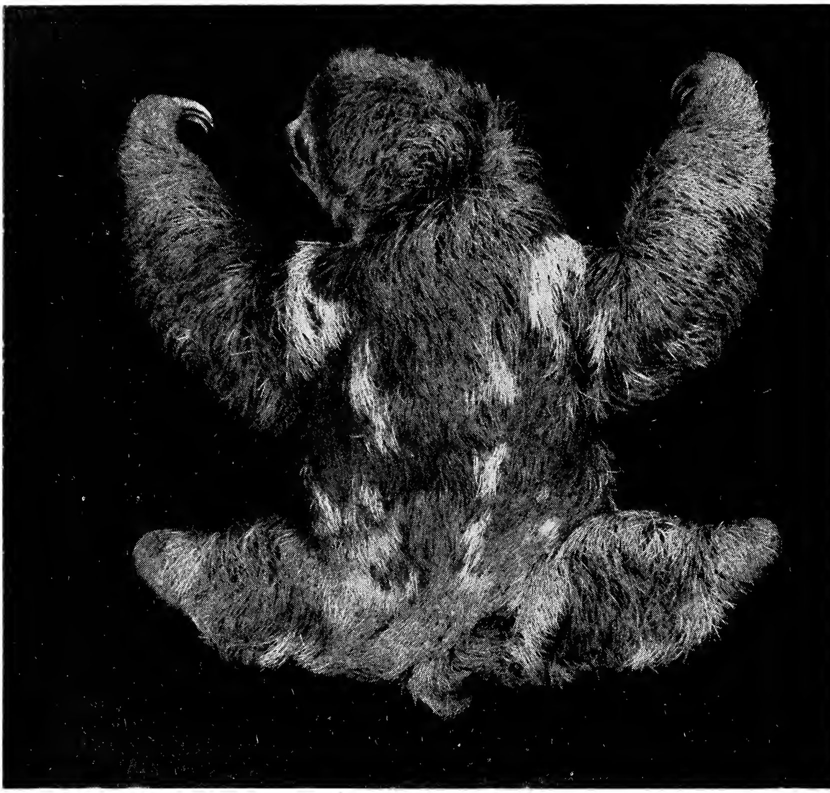


Fig. 18. Three-toed sloth, four weeks old, back view. Observe symmetry of lichen marks, lost in the adult, and different moulding of hind legs, adapted as yet to clinging to the body of the parent, rather than to climbing. Photograph by John Tee-Van.

The larynx is 35 mm. back of the snout, and the two concave cartilages are applied closely against the roof of the mouth. From the larynx down into the thorax, the trachea extends to the middle of the lungs, a distance of 95 mm., and then turns sharply upward, ventrally, back upon itself for 16 mm. It then describes a small, but complete circle also ventrally, and enters the lung tissue proper.

From the larynx to the thorax there are 52 thoracic rings, 3 mm. in diameter; from the thorax to the disappearance into the lung tissue, 48 rings, making a total of 100 tracheal rings. Looking down on the ventral aspect of the opened, undisturbed body cavity, the bladder appears very large, filling the whole lower half of the coelom between the pelvis and the sternum, diameter 33 mm., length 55 mm. The large intestine is 35 mm. in length, merging very gradually into

Fig. 19. Same as Fig. 18, lower view. Photograph by John Tee-Van.

the small intestine which is 800 mm. long and 5 mm. in diameter. The stomach occupies the upper right quarter of the visible coelom, and the intestine the upper left quarter, a superficial area of 50 by 42 by 25 mm. thick. The liver is just visible at the anterior edge of the upper left quarter. Upon examination it is found to be trilobed, 43 long, 33 wide by 12 mm. thick. The kidneys measure 18 by 13 mm.

In a two-weeks-old baby sloth the bladder is as large as in the above specimen, occupying quite half of the open, ventral, intracostal coelomic area, from the breast bone to the pelvis. Somewhat more liver is visible.

In an adult female sloth, the lungs are 85 mm. long, the larynx 50 mm. back of the snout, the recurved tracheal loop 35 mm. long. The diameter of the eyeball is 14 mm. The bladder is small, hardly

at all visible in a ventral view of the body cavity. The stomach is very large, 150 by 120 by 60 mm. thick. The liver trilobed, the whole 90 by 80 by 25 mm. thick. The complete intestinal length is 3945 mm. or just about ten feet, the large intestine alone being 120 mm. in length. The lungs are 140 by 55 by 33 mm. in depth. The trachea, from its entrance into the thorax to the lowest part of the loop, is 155 mm. long; from the loop to the top of the second turn 55 mm.; and from the thorax to the larynx 85 mm.

Early Literature

About four hundred years ago, in 1525, Gonzalo De Oviedo in his "Summarie and Generall Historie of the Indies" published perhaps the first extended account of the sloth, appearing to Purchas in his translation, a "strange beast which seemeth a kind of Camelion."

"There is another strange beast, which by a name of contrary effect, the Spaniards call Cagnuolo leggiero, that is, the Light Dogge, whereas it is one of the slowest beasts in the World and so heavie and dull in moving, that it can scarsly goe fiftie pases in a whole day; these beasts are in the firm land, and are very strange to behold for the disproportion that they have to all other beasts; they are about two spans in length when they are growne to their full bignesse, but when they are very young they are somewhat more grosse, than long; they have foure subtill feet, and in every one of them foure clawes like unto Birds, and joyned together, yet are neither their clawes or their feet able to susteine their bodies from the ground, by reason whereof, and by the heavinesse of their bodies, they draw their bellies on the ground; their necks are high and streight, and all equall like the pestle of a Morter, which is altogether equall even unto the top, without making any proportion or similitude of a head, or any difference except in the noddle, and in the tops of their neckes; they have very round faces much like unto Owles, and have a mark of their owne hairs after the manner of a Circle, which maketh their faces seeme somewhat more long than large: they have small eyes and round, and nostrils like unto Monkeyes: they have little mouthes, and moove their neckes from one side to another, as though they were astonished: their chiefe desire and delight is to cleave and sticke fast unto Trees, or some other thing whereby they may climb aloft, and therefore for the most part, these beasts are found upon Trees, whereunto cleaving fast, they mount up by little and little, staying

themselves by their long clawes: the colour of their hair is between russet and white, and of the proper colour of the haire of a Wesell: they have no tayles, and their voice is much differing from other beasts, for they sing onely in the night, and that continually from time to time, singing ever six notes one higher than another, so falling with the same, that the first note is the highest, and the other is a baser tune, as if a man should say, La, sol, fa, mi, re, ut, so this beast saith, Ha, ha, ha, ha, ha, ha. And doubtlesse, it seemeth to me, that as I have said in the Chapter of the beast called Bardati, that those beasts might be the originall and document to imbarbe Horses: even so, the first invention of Musicke might seeme by the hearing of this beast, to have the first principles of that Science, rather than by any other thing in the World. But now to return to the Historie. I say that in a short space after this Beast hath sung, and hath paused a while, shee returneth againe to the selfe-same Song, and doth this onely in the night, and not in the day: By reason whereof, and also because of her evill sight, I think her to be a night Beast, and the friend of darknesse. Sometimes the Christian men find these Beasts, and bring them home to their houses, where also they creepe all about with their naturall slownesse, insomuch that neither for threatning or pricking they will move any faster than their naturall and accustomed pace. And if they finde any Trees, they creepe thither immediately, and mount to the top of the highest branch therof, where they remayne continually for the space of eight or ten, or twentie dayes, without eating of anything, as farre as any man can judge. And whereas I my selfe have kept them in my house, I could never perceive other but that they live onely of Aire: and of the same opinion, are in manner all men of those Regions, because they have never seene them eat any thing, but ever turne their heads and mouthes toward that part where the wind blowest most, whereby may be considered that they take most pleasure in the Ayre. They bite not, nor yet can bite, having very little mouthes: they are not venemous or noyous any way, but altogether brutish, and utterly unprofitable, and without commoditie yet knowne to men, saving onely to moove their minds to contemplate the infinite power of God, who delighteth in the varietie of creatures, whereby appeareth the power of his incomprehensible wisdome and majestie, so farre to exceed the capacities of man's understanding."

Purchas presents another quaint paragraph from "Observations

gathered out of the . . . Bookes of Josephus Acosta, a learned Jesuite who wrote in 1588, touching the naturall historie of the Heavens, Ayre, Water and Earth, at the West Indies; "There is another strange beast, the which for his great heavinesse, and slownesse in mooving, they call Pericoligero, or the little light Dogge, hee hath three nailes to every hand, and mooves both hand and feete, as it were by compasse and very heavily: it is in face like to a Monkey and hath a shrill crie; it climbeth Trees, and eates Ants."

It would be interesting to know when the word Sloth or Sloath first appeared as the name of this animal. It was apparently unknown to Purchas whose "Pilgrimes" was published in 1625. Still earlier, in 1607, Topsell in his "History of Foure-footed Beastes" gives us what is perhaps the first account in the English language, under the title of Arctopithecus or Bear Ape:

"There is in America a very deformed beast, which the inhabitants call *Haut* or *Hauti*, and the Frenchmen *Guenon*, as big as a great Affrican Monkey. His belly hangeth very low, his head and face like unto a childes, and being taken, it will sigh like a young childe. His skin is of an ashe-colour, and hairie like a Beare: he hath but three clawes on a foote, as longe as foure fingers, and like the thornes of Privet, whereby he climbeth up into the highest trees, and for the most part liveth of the leaves of a certain tree, being of an exceeding heighth, which the Americans call *Amahut*, and thereof this beast is called *Haut*. Their tayle is about three fingers long, having very little haire thereon; it hath beene often tried, that though it suffer any famine, it will not eate the fleshe of a living man, and one of them was given me by a French-man, which I kept alive sixe and twenty daies, and at the last it was killed by Dogges, and in that time when I had set it abroad in the open Ayre, I observed that, although it often rained, yet was that beast never wet. When it is tame, it is very loving to a man, and desireth to climbe uppe to his shoulders, which those naked Amerycans cannot endure, by reason of the sharpnesse of his Clawes." *

The name Sloth as used for a beast does not occur in the Shakespeare Lexicon, and it may be assumed that it arose between Topsell's writing in 1607 and the first edition of Pat. Gordon's Geography in 1693. Indeed it must have been well before the latter, as school text books do not present newly coined names, but only those of

* (Quoted by J. Ashton in "Curious Creatures in Zoology," pp. 66–67, 1890.)

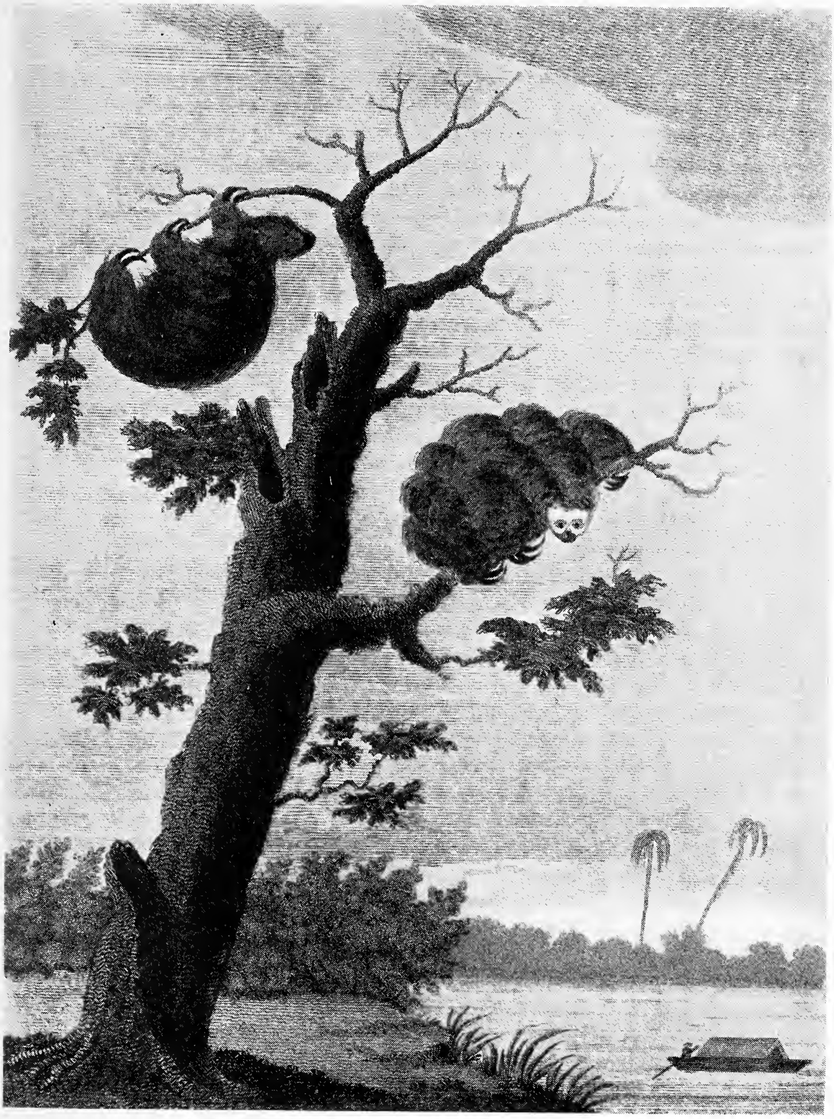


Fig. 20. Reproduction of a plate of sloths from Captain Stedman's "Narrative of a Five Years' Expedition against the Revolted Negroes of Surinam in Guiana," published in 1796.

comparatively long usage, and wide recognition. It would have come into general use after the slowness of the animal was known to be its dominant characteristic.

Pat. Gordon must have brought joy to many acquisitive minds, and sorrow to numerous schoolboys of two centuries past with his delightful "Geography Anatomiz'd." On p. 390, under rarities of Brasil, Pat. enumerates "the Sloath (term'd by the Native *Haii*, from his voice of a like Sound) but by most Europeans, *Ignavus* or *Pigritia;* and corruptedly *Pereza*, by the Spaniards; so call'd from the Nature of that Animal, being of so slow a motion, that he requires Three or Four Days to climb up a Tree of an ordinary height, and Twenty four Hours to walk Fifty Paces on plain Ground, his Fore Feet are almost double his Hinder in length and when he climbs a Tree, his hold he takes is so sure, that while he hangs by a Branch, he can sleep securely."

Purchas has preserved a paragraph from "A Treatise of Brasill, written by a Portugall" in 1601, regarding the *Priguica* or *Lazinesse.*

"The Priguica (which they call) of Brasill, is worth the seeing; it is like a shag-haire Dog, or a Land-spaniell, they are very ougly and the face is like a woman's evill drest, his fore and hinder feet are long, hee hath great clawes and cruell, they goe with the breast on the earth, and their young fast to their bellie. Though yee strike it never so fast it goeth so leasurely that it hath need of a long time to get up into a tree, and so they are easily taken; their food is certaine Fig-tree leaves, and therefore they cannot be brought to Portugall, for as soone as they want them they die presently."

A few decades later, in 1796, we have Capt. J. G. Stedman "Narrative of a Five Years' Expedition against the Revolted Negroes of Surinam in Guiana," wherein he illustrates (page 153) both the Two- and Three-toed Sloth with such naive charm that I have reproduced the engraving, on page 59 of this paper.

His account of the habits of the sloth are far less accurate and more fanciful than those of De Ovieda, written 271 years earlier. He says, "My negroes . . . brought on board a poor animal alive, with all its four feet chopped off with the bill-hook, and which lay still in the bottom of the canoe. Having freed it from its torment by a blow on the head, I was acquainted that this was the *sloth*, called *loyaree* or *heay* by the natives on account of its plaintive voice. It is about the size of a small water-spaniel, with a round head something like that of a monkey, but its mouth is remarkably large; its

hinder legs are much shorter than those before, to help it in climbing, being each armed with *three* very large and sharp claws, by which it holds its body on the boughs, but which, as being offensive weapons, my negroes had so cruelly chopped off; its eyes are languid, and its voice is squeaking, like that of a young cat. The greatest particularity of this creature however is, that its motion is so very slow, that it often takes two days to get up to the top of a moderate tree, from this it never descends while a leaf or a bud is remaining; beginning its devastation first at the top, to prevent its being starved in coming to the bottom, when it goes in quest of another, proceeding incredibly slow indeed while on the ground. Some say, that to avoid the pain of exercising its limbs, it forms itself into a ball, and drops down from the branches: that may be true or not, but this I know to be a fact, that it cannot mend its pace.

Of these animals there are two species in Guiana, viz. the *Ai* and the *Unan;* but in Surinam distinguished by the names of the *Sicapo* and *Dago luyaree,* or the Sheep and the Dog Sloth, on account of their hair; that of the first being bushy, and of a dirty grey, while the other is lank and reddish-coloured. This last has also but *two* claws on each foot, and the head is less round than the former. Both these creatures, by forming themselves in a clew, have often more the appearance of excrescences in the bark, than that of animals feeding upon the foliage, which frequently prevents them from being discovered by the natives and negroes, who devour their flesh with avidity."

The early Dutch settlers of Guiana were by no means unobservant, and if we had more of their letters, and if reports had been preserved, we would doubtless find many references to sloths. Jan Jacob Hartsinck published two large volumes in 1770 entitled "Beschryving van Guiana," and on page 95 he has an illuminating paragraph on the *Ai* or *Haji.* This very page in a copy of the work which was presented to me by James Rodway, Esq., of the Georgetown Museum, shows so well the enthusiasm of arthropod book worms, and the trials of vertebrate ones in the tropics, that I have reproduced it.

Hartsinck's paragraph translated reads, "The most curious of all the quadrupeds of this country is the *Ai* or *Haji,* thus called by the Indians on account of the noise coming from its throat, but by us going by the name of Sluggard (Luyaard). This name it deserves for the slothfulness of its movements, as it requires two or three

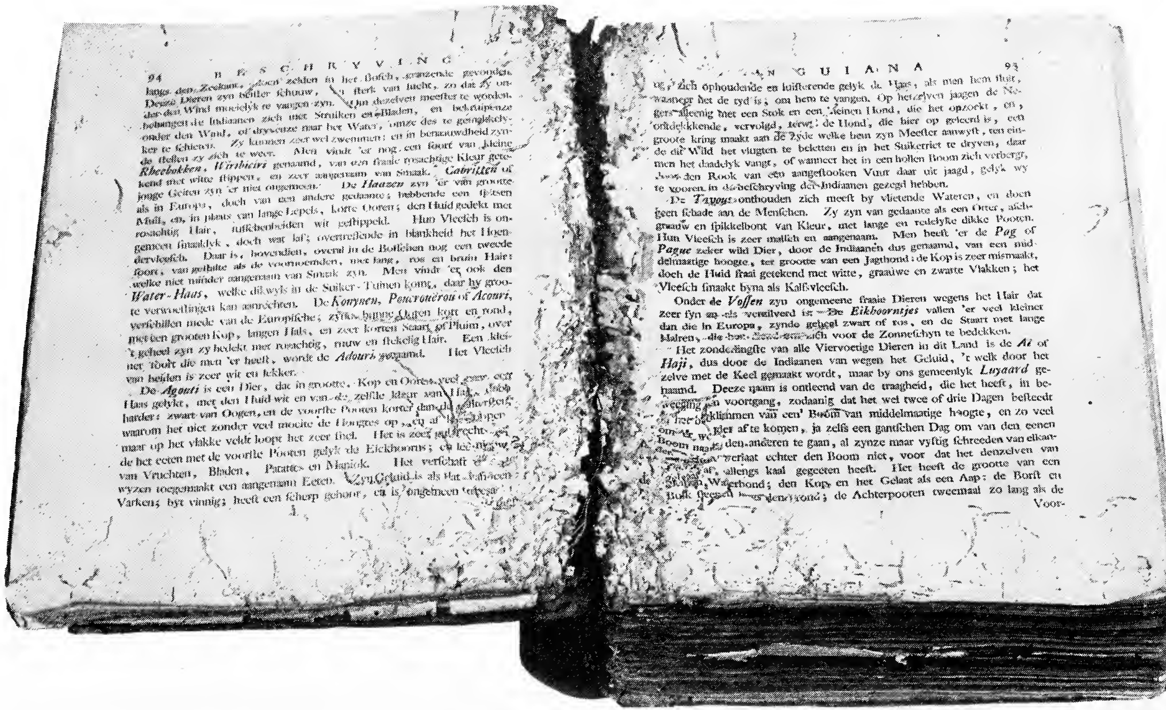
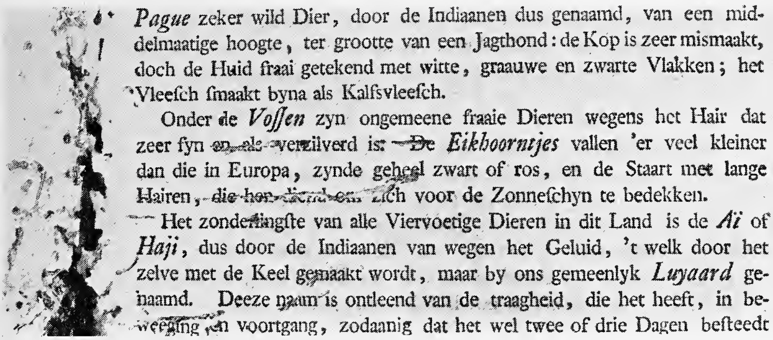


Fig. 21. An old Dutch book of the period of 1770 showing the damage done by insects of the Tropics.

days to climb trees of a medium height, and as many again to come down. They even employ a whole day to go from one tree to another, though but fifty paces apart; it will not quit the tree until it



Pague zeker wild Dier, door de Indiaanen dus genaamd, van een middelmaatige hoogte, ter grootte van een Jagthond: de Kop is zeer mismaakt, doch de Huid fraai getekend met witte, graauwe en zwarte Vlakken; het Vleeſch ſmaakt byna als Kalfsvleeſch.

Onder de *Voſſen* zyn ongemeene fraaie Dieren wegens het Hair dat zeer fyn en als verzilverd is: De *Eikhoorntjes* vallen 'er veel kleiner dan die in Europa, zynde geheel zwart of ros, en de Staart met lange Hairen, die hen dienen, zich voor de Zonneſchyn te bedekken.

Het zonderlingſte van alle Viervoetige Dieren in dit Land is de *Ai* of *Haji*, dus door de Indiaanen van wegen het Geluid, 't welk door het zelve met de Keel gemaakt wordt, maar by ons gemeenlyk *Luyaard* genaamd. Deeze naam is ontleend van de traagheid, die het heeft, in beweeging en voortgang, zodaanig dat het wel twee of drie Dagen beſteedt

Fig. 22. A section of right hand page of Fig. 21, with an account of sloths observed by the Author in Dutch Guiana.

has eaten it bare from top to bottom. It is of the size of a small dog, with the head and face like a monkey. The chest and belly they drag along the ground; the hindmost legs are twice as long as the forelegs, which it keeps asunder like a frog. To each leg are attached three crooked nails, which are so powerful that one is obliged to use the greatest violence to make it let go whatever it has laid hold of. These at the same time serve it to climb the trees; it has moreover this peculiarity that it laughs and cries like an infant at one and the same time. It belongs to the race of Monkeys."

Edward Bancroft in his "Essay on the Natural History of Guiana," published in 1769, reaches the lowest level of secondhand acceptance of fanciful tales. He says: "The Sloth is also common in Guiana, being of the size of a Fox; its fore feet are longer than those behind, and each foot has three claws. But the peculiar characteristic of this animal is, his insuperable aversion to motion, being of all animals the most indolent and inactive: Upon level ground they are unable to move above forty or fifty paces in a day, and whenever they ascend a tree, never leave it whilst either fruit or leaf is remaining. When by beating they are forced to move, they make the most melancholy pityful noise and grimaces. But as these animals are common to all parts of America between the Tropics, and have been repeatedly described, I shall not enter into a more particular description of them."

Fig. 23. Adult male two-toed sloth. Observe equal length of limbs, more projecting muzzle and less developed tail. Photograph by Elwin R. Sanborn.

The accounts of Bancroft, Stedman and others of their ilk evidently moved Waterton to the general condemnation of the so-called naturalists of his time, and to his humorous perpetration of his famous "Nondescript."

Concerning the Three-toed Sloth he says, "Those who have written on this singular animal, have remarked that he is in a perpetual state of pain, that he is proverbially slow in his movements, that he is a prisoner in space, and that as soon as he has consumed all the leaves of the tree which he had mounted, he rolls himself up in the form of a ball, and then falls to the ground. This is not the case."

And again "The sloth is as much at a loss to proceed on his journey upon a smooth and level floor, as a man would be who had to walk a mile on stilts upon a line of featherbeds."

Nevertheless Waterton himself judged too much of his sloth's habits from its sleeping on a chair back, and is far astray in his description of the animal's sleeping posture, and of the uselessness of its tail.

NOTES ON *Choloepus didactylus* Linné TWO-TOED SLOTH.

While I shall reserve detailed treatment of this second species of sloth for a later paper, it seems worth while to present a few of the most important contrasts between it and the Three-toed *Bradypus*.

An adult female, after two months in captivity, has become very tame, making no effort to strike with its claws, but only a gentle tug to draw one's hand to its mouth. When much annoyed, it opens its mouth wide and tries feebly to bite, and could probably do damage, as its teeth are so much longer and sharper than those of *Bradypus*. Three other newly caught individuals were extremely savage and active, infinitely more dangerous than Three-toed Sloths ever are.

The two species of sloths, physically and psychologically, are much more than generically separated. They are wholly unlike in every way. In activity and general correlation the two-toed is about three times as developed as the other animal.

The eyes are larger and the optical divergence is 34°. The nose is the most prominent feature, and the nostrils large and flaring, while the whole of the surrounding skin is constantly moist. Although the movements are slow in comparison with other types of animals, they are about three times as rapid and as correlated as those of the three-toed species.

The head is constantly moved about, the attention is more concentrated, as to eye and ear at least. Over the ground this is especially noticeable and when going steadily over ground with good gripping facilities, such as short grass, the animal actually walks upright, or on all four soles, with the hind legs gathered beneath it, and the entire body clear of the ground. The head is raised high, now and then dropping the muzzle to the ground. Poor as the eyesight is, the direction is chosen after a survey of the surroundings.

The difference in direction of the hair on some portions of the body, and the total absence of a tail, indicate radical changes in arboreal mode of life.

The two toes on the fore feet and the narrow, elongated foot indicate specialization for arboreal life comparable with the anterior limbs of the spider monkeys and gibbons, but the bare sole is more generalized than the hair-covered foot of *Bradypus*.

The hair is much finer and longer than that of the three-toed, and there is less of a dense under-coat. The absence of this defense is perhaps compensated for by the increased activity and, (as observed in other individuals) a greatly enhanced ability to defend itself by strength and mobility of claws, and activity of head and neck, and length and sharpness of teeth.

In eating, this sloth shows a remarkable skill in manipulating the leaf-bearing branches. One is pulled toward its mouth and when it breaks off, the stem is held daintily in the grip of the claws against the palm, and is turned and pushed forward as the leaflets are devoured. This animal will take wild plum leaves called hog-plum or "hobo" from the hand.

In sleeping, it descends and rests its whole back on the floor of the cage and curls up into a ball.

A most interesting character is that when it decides to descend a tree-trunk or branch it turns around and comes down head first, with the body quite free of the trunk, not half clinging, half sliding tail first, as the three-toed do.

No sound but a low hiss, uttered when suddenly disturbed, has been heard.

The male lacks the bright colored dorsal spot and the general coloration is light grey. In detail the hair around the face is light ochraceous buff, shading up on the forehead through greyish olive to mummy brown at the back of the head. The back of the neck and

shoulders are light grey tinged with algal green; limbs cinnamon brown; back generally tilleul buff, becoming buffy on ventral surface and darker toward tail; soles dark vinaceous drab with a few large coarse, flesh-colored markings; eye tawny olive.

EARLY LITERATURE

ASHTON, JOHN.

1890. Curious Creatures in Zoology. (Frederick Warne & Co., Bedford Street, Strand, London.)

BANCROFT, EDWARD.

1749. An essay on the Natural History of Guiana, in South America. (T. Becket & P. A. De Hondt.)

GORDON, PAT.

1708. Geography Anatomiz'd: or The Geographical Grammar. (Printed for John Nicholson, John Sprint, and S. Burroughs, in Little Britain; Andr. Ball at the Cross-Keys and Bible in Cornhill, & R. Smith under the Royal Exchange.)

PURCHAS, SAMUEL.

1906. Hakluytus Posthumus, or Purchas His Pilgrimes. (James Mac Lehose & Sons, Glasgow.)

STEDMAN, CAPT, J. G.

1796. Narrative of a Five Years' Expedition against the revolted Negroes of Surinam, from 1772 to 1777. (J. Johnson, St. Paul's Church Yard, and J. Edwards, Pall Mall.)

WATERTON, CHARLES.

1870. Natural History Essays. (Frederick Warne & Co., Bedford St., Strand, London.)

1852. Wanderings in South America. (B. Fellowes, Ludgate Street, London.)

New York Zoological Society

OBJECTS OF THE SOCIETY

A Public Zoological Park. A Public Aquarium The Preservation of our Native Animals. The Promotion of Zoology.

ZOOLOGICA VOL. I

	Paper	Cloth
1—Geographic Variation in Birds (*Beebe*)	.30	
2-3—Ecology of the Hoatzin; Birds of Venezuela (*Beebe*)	.50	
4—New Species of Insects (*Beebe*)	.25	
5-6—Racket Formation, Tail-Feathers; Supernumerary Toe, Hawks (*Beebe*)	.25	
7—Juvenal Plumage, Yucatan Jay (*Beebe*)	.15	
8—Northern Elephant Seal (*Townsend*)	.25	
9—Affections of Respiratory and Digestive Organs, Primates (*Blair*)	.15	
10—New Blood Pheasant (*Beebe*)	.15	
11—Feeding Habits, Serpents (*Ditmars*)	.50	
12-13-14—Ontogeny, the White Ibis; Specialization, Tail-down in Ducks; Postponed Moult, Certain Passerines (*Beebe*)	.25	
15—Pheasant Studies (*Beebe*)	.25	
16—Porpoise in Captivity (*Townsend*)	.25	
17-18—The Genus Gennaeus (*Beebe*) Notes on Costa Rican Birds (*Crandall*)	.25	
19—Natural History, Whale Shark (*Gudger*)	.30	
20—Ectoparasitic Trematodes (*MacCallum*)	.25	

Postage, Zoologica, 5 cents

	Paper	Cloth
Parts 1-20 ... *Not bound*	3.85	
Parts 1-20 ... *Bound*		6.00

Postage-weight, 4 pounds

ZOOLOGICA VOL. II

1—Two Series of Amphibians (*Deckert*)	.25
2—Tetrapteryx Stage, Ancestry Birds (*Beebe*)	.25
3-4—Notes, Birds, Para, Brazil; Fauna of Jungle Debris (*Beebe*)	.25
5—The Gaff-Topsail Catfish (*Gudger*)	.25
6—Mammals of Australia in the Zoological Park (*W. H. D. Le Souef*)	.75
7-8-9—Vertebrates, British Guiana (*Beebe*)	.25
10—Habits of Sage Grouse (*Horsfall*)	.25
11—Eclipse Plumage, Domestic Fowl (*Crandall*)	.25
12—Life History of the Puffer (*Welsh-Breder*)	.25
13—Hermaphroditism of the Croaker (*Breder*)	.25
14—Food of Certain Minnows (*Breder-Crawford*)	.25
15—Fishes of Sandy Hook Bay (*Breder*)	.25
16—Weaving of Weaver Birds (*Friedman*)	.25
17—Scales of Whitefishes (*Mellen-Van Oosten*)	.30
18—The Anderson Tree Frog (*Noble*)	.25

Postage, Zoologica, 5 cents

ZOOLOGICA VOL. III

	Paper	Cloth
1–2—Objects, Tropical Research Station (*Osborn*)	.25	
Contributions Tropical Research Station (*Beebe*)		
3–11—Social Beetles, British Guiana (*Wheeler*)		
Tachigalia Ants (*Wheeler*)		
Habits of Cucujidae (*Wheeler*)		
New Coleoptera (*Schwarz-Barber*)		
Larvae, Pupae, Social Beetles (*Boving*)		
New Diadiplosis (*Felt*)		
New Blepyrus (*Brues*)		
Tachigalia Membracids (*Herbert Osborn*)		
New Entomobrya (*Folsom*)	1.00	
12—Fetuses, Guiana Howling Monkey (*Schultz*)	.50	
13—Mammals Collected Tropical Research Sta. (*Anthony*)	.25	
14–15—New Batrachians (*Noble*). New Lizards (*Noble*)	.25	
16—Descriptiones Termitum in Anglorum Guiana Reportorum (*Silvestri*)		
17—New Genera and Species, Termitophilous Coleoptera (*Mann*)		
18—Glandular Structure, Abdominal Appendages, Termite Guest (*McIndoo*)		
19—Termitophilous Apterygota (*Folsom*)		
20—Three Apparently New Species, Termitaphis (*Morrison*)		
21—Termitophilous Millipeds (*Chamberlin*)	.75	
22–23—A Termitophilous Braconid (*Brues*). Two Myrmecophilous Phoridae (*Brues*)	.25	

Postage, Zoologica, 5 cents

ZOOLOGICA VOL. IV

	Paper	Cloth
1—Fishes, Amphibians, Reptiles (*Breder*)	.15	
2—Frozen Mammoths (*Lang*)	.25	
3—Galapagos Tortoises (*Townsend*)	.50	
4—Some Panama Fishes (*Breder*)	.20	

ZOOLOGICA VOL. V

	Paper	Cloth
1—Williams Galapagos Expedition (*Beebe*)	.15	
2—Galapagos Heterocera (*Schaus*)	.20	
3—Galapagos Lepidoptera (*Beebe*)	.15	
4–16—Ichthyology (*Nichols*)		
Apterygota (*Folsom*)		
Homoptera (*Osborn*)		
Mallophaga (*Ewing*)		
Diptera (*Johnson*)		
Arachnida (*Banks*)		
Formicidae (*Wheeler*)		
Triungulin Larvae (*Brues*)		
Chilopods (*Chamberlin*)		
Coccidae (*Morrison*)		
Brachyuran Crabs (*Rathbun*)		
Macrura and Anomura (*Schmitt*)		
Hymenoptera (*Rohwer*)	.50	
17—Neuroptera (*Banks*)	.15	
18—Isopods (*Van Name*)	.25	
19—Copepods (*Wilson*)	.15	
20—Coleoptera (*Mutchler*)	.20	
21—Hemiptera-Heteroptera (*Barber*)	.15	

ZOOLOGICA VOL. VI

	Paper	Cloth
1—Ecology of Kartabo (*Beebe*)	1.00	
2—Birds of Kartabo (*Beebe*)	.35	
3—Membracidae of Kartabo (*Haviland*)	.30	
4—Termites of Kartabo (*Emerson*)	1.00	
5—Ispods of Kartabo (*Van Name*)	.30	

Publications of the Society for sale at the Zoological Park, 185th Street and Southern Boulevard, New York City.

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

DEPARTMENT OF TROPICAL RESEARCH
KARTABO, BRITISH GUIANA

VOLUME VII. NUMBER 2

Department of Tropical Research Contribution Number 244

DEVELOPMENT OF SOLDIER TERMITES

BY ALFRED EDWARDS EMERSON

University of Pittsburgh

PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

November 12, 1926

DEVELOPMENT OF A SOLDIER
Of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) AND ITS PHYLOGENETIC SIGNIFICANCE*[1]

By Alfred Edwards Emerson

University of Pittsburgh

(Figs. 24–32 incl.)

OUTLINE

Introduction

During my studies on the life of termites at Kartabo, British Guiana, I happened, by chance, to find a molting termite in a nest of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) (Fig. 26) which appeared to be a nasuate soldier emerging from a pigmented worker skin. I had been carefully searching the nest for a remarkable termitophilous Staphylinid, *Spirachtha*, but realizing the significance of my chance discovery, I continued to hunt for molting individuals. Altogether, during my studies in British Guiana, I found about six specimens, most of which (Fig. 27, *b*) were in the middle of the process. In addition to these molting specimens, I fixed a large number of workers, soldiers and nymphs of this species in Bouin-Dubose, Gilson's, Hot Corrosive Sublimate and Alcohol. This

* Thesis presented to the faculty of the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[1] Contribution, N. Y. Zool Soc. Department of Tropical Research No. 244

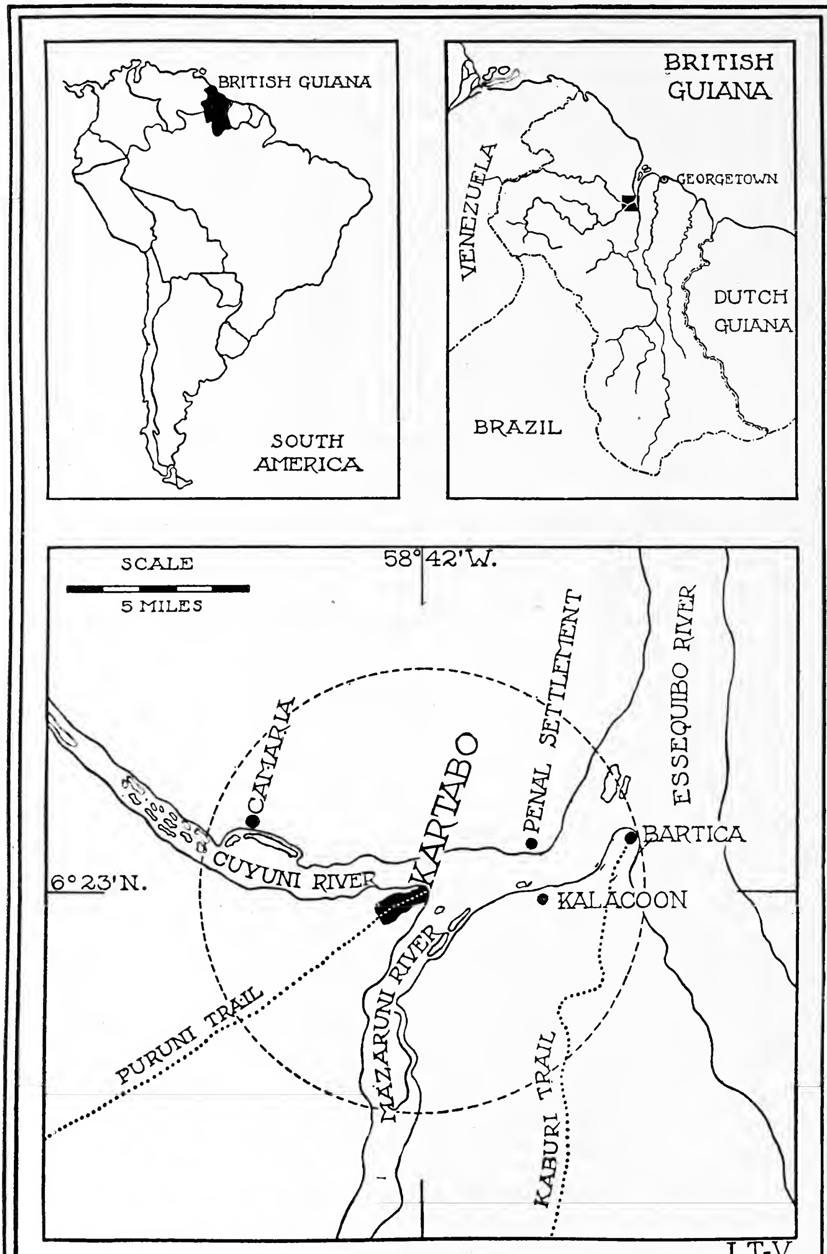


Plate A. British Guiana Tropical Research Station of the New York Zoological Society. Circle represents a radius of six miles.

material forms the basis of this report. About twenty insects were sectioned and stained, making about sixty slides.

The work has been done under the direction of Dr. O. A. Johannsen of Cornell University to whom I am immensely indebted for his advice and suggestions. I wish also to take this occasion to thank Professor H. D. Fish of the University of Pittsburgh for his interest in this problem and for the many hours in which we discussed various theories to account for the facts presented. I am also indebted to Dr. Caroline B. Thompson and Dr. T. E. Snyder for their interest and valuable suggestions. It was my great misfortune not to be able to personally talk over the problem with Dr. Thompson before her untimely death in December 1921.

Problem

My purpose has been to answer the following questions related to the discovery of the molting individuals:

1. What is the caste of the individual before it molts? Is it a true worker, or can it be distinguished from the true worker?
2. What are the internal and external changes which take place during this metamorphosis?
3. In what way does this metamorphosis help to explain the phylogenetic development of the castes in question?

Ontogenetic Development of Castes

Many writers, particularly the early students of polymorphism among the social insects, have believed that food was either a direct cause of caste production or else served to stimulate or inhibit the development of the different castes from undifferentiated young.

The observations of the following authors, historically reviewed by Thompson (1917) have supported this hypothesis: Lespès (1856), Müller (1873–75), Weismann (1892, 1893, 1894, 1902), Spencer (1893–94), Grassi and Sandias (1893–94), Emery (1893, 1896, 1904, 1910), Silvestri (1902, 1903), Desneux (1904), Escherich (1909), Holmgren (1909) and Feytaud (1912). Jucci (1920, 1924, 1925) also supports this theory.

The belief that the intestinal protozoa influence caste production in termites was advanced by Grassi and Sandias (1893–94). This theory has been completely refuted by the work of Imms (1919) and Cleveland (1923, 1923a, 1924, 1925, 1925a, 1925b).

The following authors have contributed to the belief that the castes are already predetermined at the time of hatching and are not due to food or its influence:

Bobe-Moreau (1843) states that he was able to distinguish soldier nymphs among newly hatched forms. This is probably an erroneous observation.

Hagen (1855–60) quotes Bates, who was then in Brazil, as saying that he believed that the castes were not undifferentiated at the time of hatching, but that the sexual forms were distinct from the others. His belief lay, not in observing any differences in the newly hatched nymphs, but in the fact that all types were found in the nests together in the same cells, and that it seemed unlikely that special food could be administered to any particular group.

Dewitz (1878) believes that the eggs must be predetermined within the body of the mother.

Knower (1894) observed the molt from a worker-like nymph into a nasuate soldier in a species of *Nasutitermes* determined later by Banks as *N. pilifrons*. Knower found a nymph with 13 antennal segments, which was worker-like in its head and jaws, but possessed a small frontal gland. This form molted into a nasuate soldier.

Wheeler (1907) makes the following statement with regard to ants.

"While experiments on many organisms have shown that the quality of assimilated food may produce great changes in size of stature, there is practically nothing to show that even very great differences in the quality of the food can bring about morphological differences of such magnitude as those which separate the queens and workers of many ants.

". . . It must be admitted that a direct causal connection between underfeeding on the one hand and the ontogenetic loss or development of characters on the other, has not been satisfactorily established. The conditions in the termites, which are often cited as furnishing proof of this connection, are even more complicated and obscure than those of the social Hymenoptera."

Bugnion (1912a) states that he found an individual, 1.3 mm. long, with a distinct frontal projection, frontal gland and duct, among a number of newly hatched nymphs of "*Eutermes*" (= *Nasutitermes*) *lacustris*. In correspondence with Miss Thompson, however, he writes that he now believes that he was mistaken. He very likely mistook the long labrum for the nose, which it resembles in the early stages, and confused the frontal gland with the brain (Thompson, 1919).

Snyder (1915) observed and figured the change from worker-like nymphs to soldiers. He makes the following statement with regard to *Reticulitermes flavipes* and *R. virginicus:*

"In the development of the soldier, however, marked changes in form occur, the mature soldier, with pigmented head and saber-like mandibles, being developed from a large-headed, white, worker-like larva."

Thompson (1917), in commenting upon this observation of Snyder's, says:

"This fact proves for *Leucotermes* (= *Reticulitermes*), as Knower's work did for *Eutermes* (= *Nasutitermes*), that the worker-like nymph from which the soldier develops resembles the worker in external characters only, but internally possesses the distinctive organs of the soldier caste."

In my opinion, Thompson's (1917) paper on the origin of castes in *Reticulitermes* stands out as the most important work on this problem which has yet been done. She traces the development of species of this genus very carefully from their emergence from the egg. Her summary at the end of the paper is as follows:

"1. The newly hatched nymphs of *L. flavipes* and *L. virginicus* are externally all alike, but internally there are marked structural differences which divide the nymphs into two sharply defined types, the reproductive and the worker-soldier types, which are respectively the prototypes of the 'small headed' and 'large headed' nymphs of Grassi. Therefore, the fertile and sterile types are predetermined at the time of hatching.

"2. The two types of newly hatched nymphs may be distinguished by the following characters: a, the bulk of the brain; b, the relative size of brain and head; c, the structure of the compound eyes; and d, the size of the sex organs.

"3. The reproductive type of newly hatched nymph has a large brain, in which the mushroom bodies, optic lobes and antennary lobes are all large. The space within the hypodermis of the head is nearly filled by the brain. The compound eyes are slightly larger and more differentiated, and the sex organs are larger than in the worker-soldier type.

"4. The worker-soldier type of newly hatched nymph has a small brain, with small mushroom bodies, optic lobes and antennary lobes. The space within the hypodermis of the head is not nearly filled by the brain. The compound eyes are smaller and simpler, and the sex organs are smaller than in the reproductive type.

"5. The antennae of the newly hatched nymphs of both *L. flavipes* and *L. virginicus* are composed of nine segments, the third segment grooved and bare.

"6. In nymphs of *L. flavipes* with ten antennary segments, the third segment grooved, and a body length of 1.3 to 1.4 mm., the individuals of the reproductive type are further differentiated into two groups: a, with large brain and large sex organs; b, with slightly smaller brain and smaller sex organs.

These are the respective prototypes of the nymphs of the first form and the nymphs of the second form, and hence of the two adult castes of the first form, with long wings, and of the second form, with short wing pads.

"7. The prototypes of the worker and soldier castes, although externally alike, are distinguishable by internal structures at the end of the second stage of development, in nymphs with a body length of 3.75 mm., and are probably distinguishable at an even earlier age.

"8. The frontal gland is present, although barely recognizable, in the newly hatched nymphs, and grows larger and more complex as development proceeds. The fontanelle nerve (median ocellar nerve) is not present in the earlier phases, but is clearly seen in individuals with a body length of 1.6 mm. From the beginning, the frontal gland is larger and more differentiated in individuals of the reproductive type than in the worker-soldier type, and may be added to the list of characters by which the two types are distinguished. In individuals of the large headed worker-soldier type, with a body length of 3.75 mm. two types of frontal glands may be recognized: a small, primitive frontal gland in the worker prototypes, a large, highly modified gland in the soldier prototypes.

"9. No evidences of a prototype for the third adult reproductive caste, without wing pads, have been seen in this study of the development of *L. flavipes*.

"10. To simplify the heterogeneous nomenclature of the three adult reproductive castes I have suggested the following terms, which are in conformity with the terms applied to the oldest nymphs since the time of Lespès (1856):

1. Adults of the first form, or males and queens of the first form (with long wings or stubs of wings).

2. Adults of the second form, or males and queens of the second form (with short wing pads).

3. Adults of the third form, or males and queens of the third form (with no wing pads)."

In another paper, Thompson (1919) continues this study on other genera and species of termites with the same general conclusions. The work on a species of *Nasutitermes* (*N. pilifrons*), called *Eutermes* in the paper, is of particular interest in connection with the observations which I am presenting in the following pages. *Nasutitermes pilifrons* belongs to the subgenus *Nasutitermes* s. str. and is not very closely related to the species of the subgenus *Constrictotermes*. Miss Thompson's observations are as follows:

"*E.* (= *Nasutitermes*) *pilifrons* like all the other termites described in this paper, has the two types of newly hatched nymphs which are alike in external structure:—the reproductive nymphs with a large brain and large sex organs, and the worker-soldier nymphs, with smaller brain and smaller sex organs. . . .

"In worker-soldier individuals about 2 mm. long and with twelve antennal segments there is as yet no external differentiation between the two sterile castes, but an internal differentiation has already begun and may be observed in

whole mounts of stained individuals as well as in sections. The future soldiers are distinguishable by the presence of the larger frontal gland which appears, in frontal mounts of the head, as a small dense spot posterior to the brain; in whole mounts of the head of the future worker no such spot is visible. After examining the stained specimens in cedar oil to separate the future soldiers from the future workers, the two kinds of individuals were embedded and sectioned. In the soldier nymphs a large, although embryonic, frontal gland opens to the exterior on the frontal surface of the head. This gland was more than three times the size of the vestigial gland found in the worker nymphs.

"The soldier caste of *E. pilifrons* is, therefore, not differentiated by external characters at the time of hatching, but arises later in development, being first manifested in individuals about 2 mm. long with twelve antennal segments. The worker caste is differentiated at the same time, and the two castes may be recognized by the size and structure of the respective frontal glands; although no external differentiations are yet present in either caste.

"The differentiation of the worker-soldier nymphs of *E. pilifrons* into the worker and the soldier is nearly parallel with the development of these two castes from the worker-soldier form in the genus *Reticulitermes*, the chief difference being the age of the respective nymphs, the differentiation being visible in *E. pilifrons* in nymphs 3.75 mm. long, although, from the maturity of the frontal gland, it could probably be seen in an earlier phase."

Imms (1919) also believed that nutrition could not be a causal factor in producing polymorphism in termites and indicated his strong belief in intrinsic factors which predetermined the caste in the egg.

Snyder (1925) brings many biological facts together to disprove the theory that food can influence caste production.

It is the writer's opinion that the careful work of these authors, particularly that of Miss Thompson, strongly indicates that all termite castes are predetermined in the egg.

Development of a Soldier of *Nasutitermes* (*Constrictotermes*) *cavifrons*

The case described in the following pages differs from the development already referred to by Knower (1894) and Thompson (1917, 1919) in that the nasuate soldier molts from a fully pigmented form which not only resembles the normal mature worker, but functions as such in the social life of the colony. The worker-like nymphs formerly described were either white or else only slightly pigmented, and it has never been thought, as far as I am aware, that they functioned as workers except in the case of the *Kalotermitidae*.

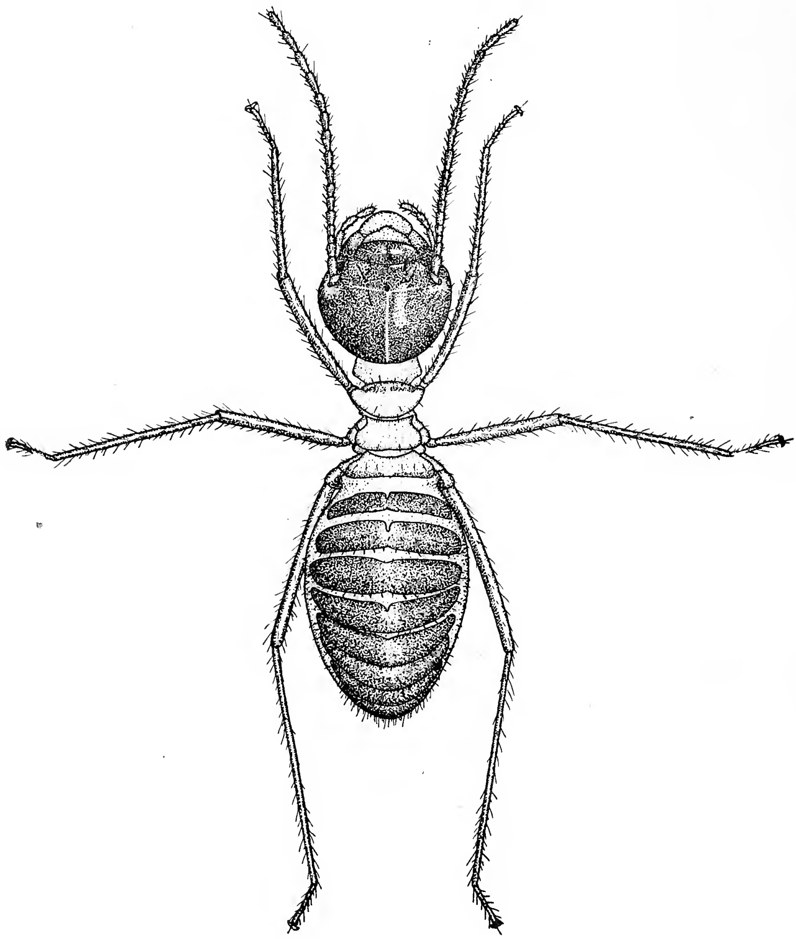


Fig. 24. Small pigmented, work-like form of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) which later changes into a soldier.

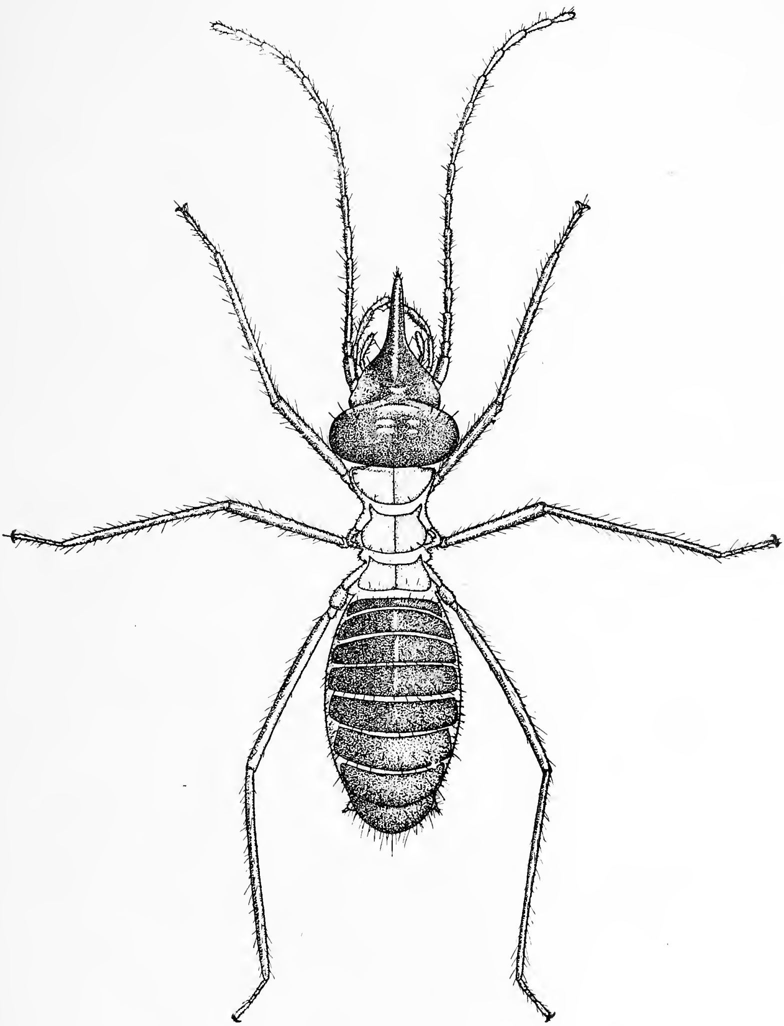


Fig. 25. Mature, pigmented soldier of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren).

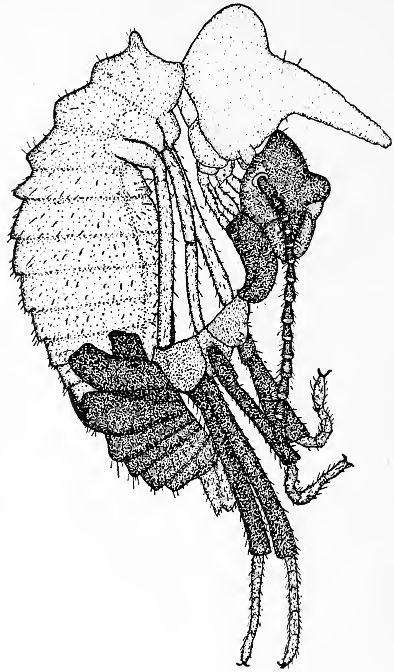


Fig. 26. Nasuate soldier nymph emerging from a pigmented, work-like skin.

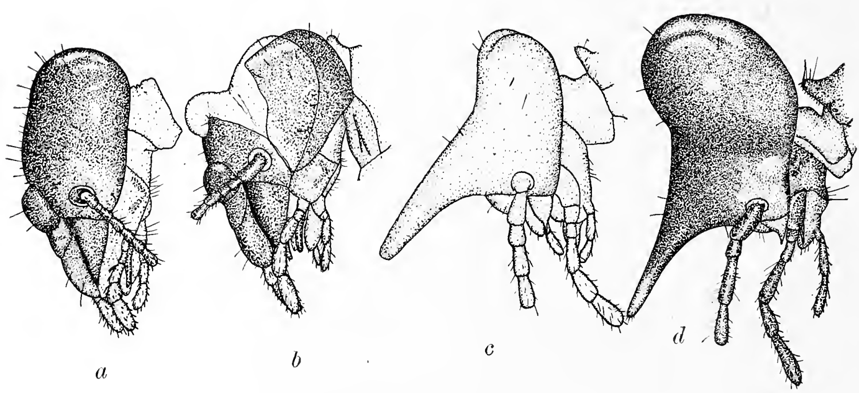


Fig. 27. *a*, Side view of the head of a small, pigmented worker-like form; *b*, molting, individual showing the nose starting to push out through the split Y-suture; *c*, nasuate soldier nymph after change from small, pigmented work-like form; *d*, mature, pigmented soldier.

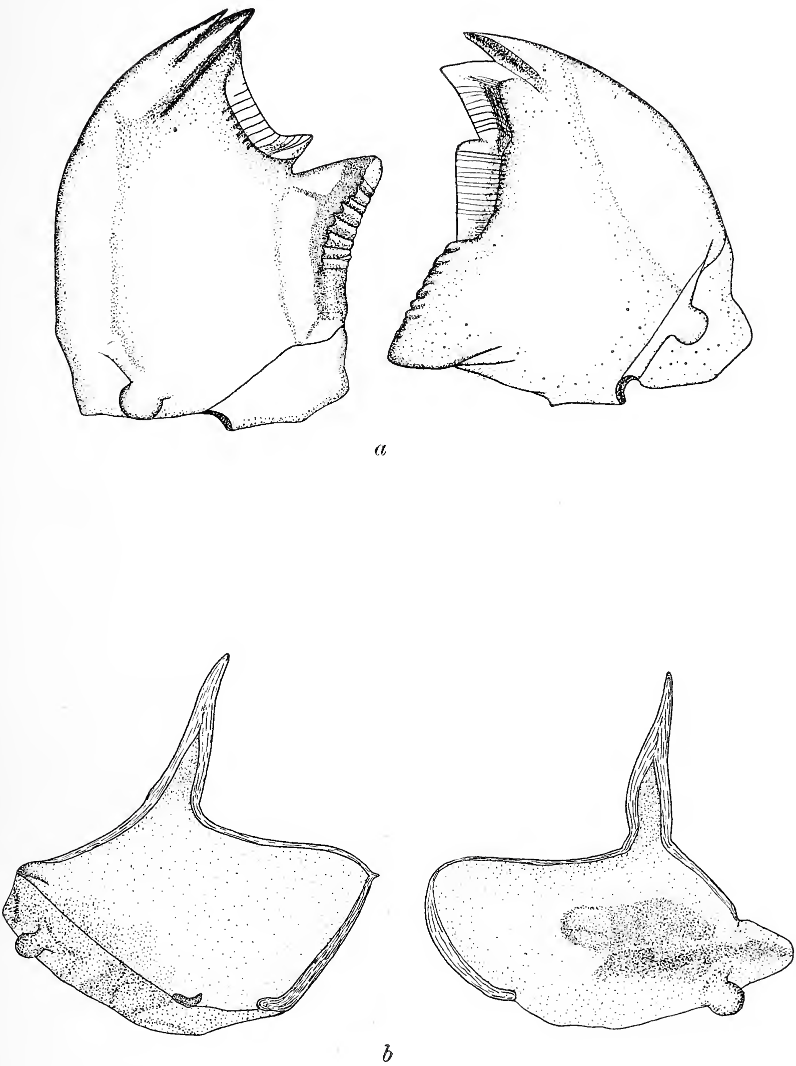
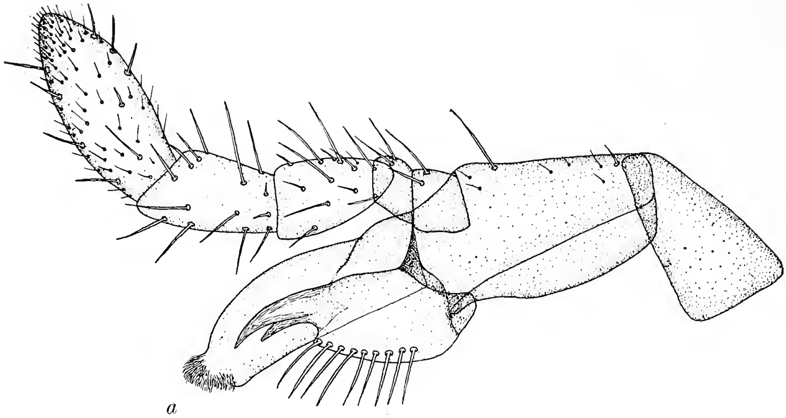
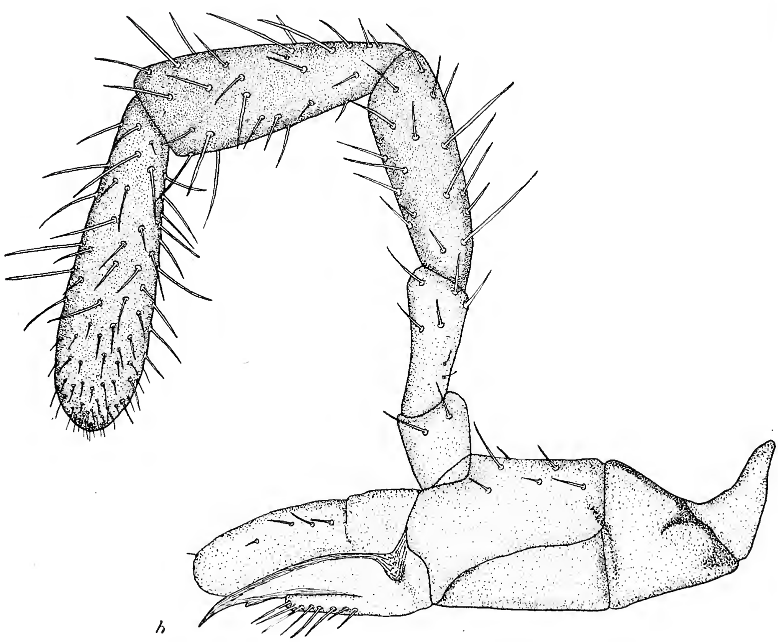


Fig. 28. *a*, Mandibles of a small, pigmented, worker-like form; *b*, mandibles of a mature, pigmented soldier.

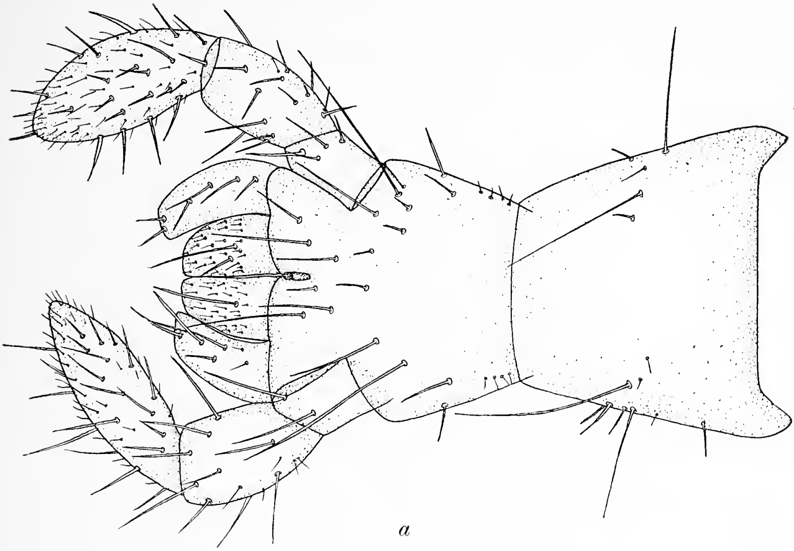


a

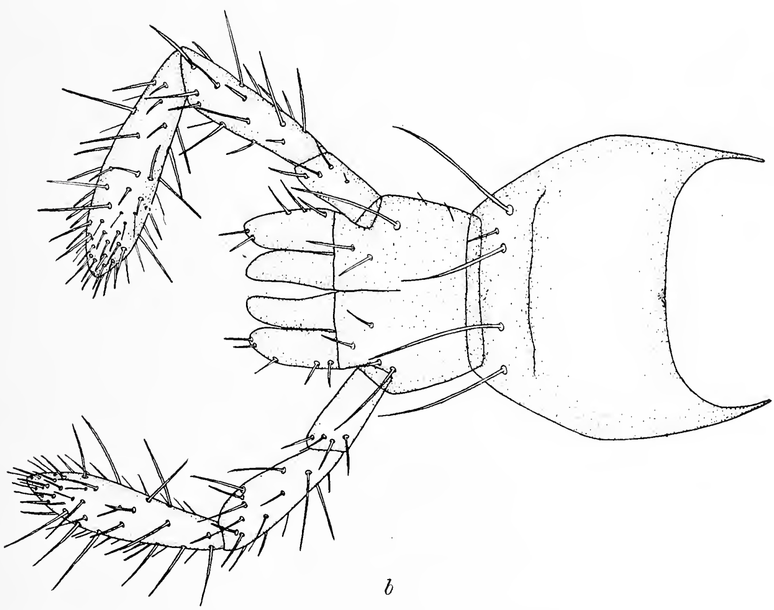


b

Fig. 29. *a*, Maxilla of a small, pigmented, worker-like form; *b*, maxilla of a mature, pigmented soldier.

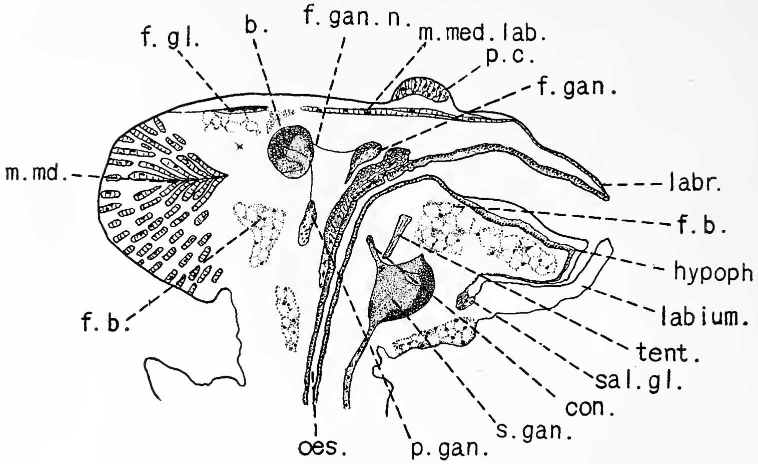


a

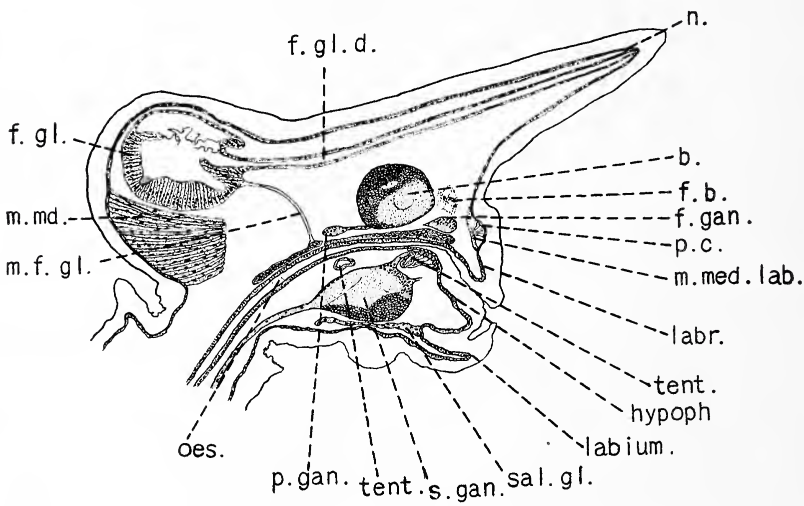


b

Fig. 30. *a*, Labium of a small, pigmented, worker-like form; *b*, Labium of a mature, pigmented soldier.



a



b

Fig. 31. *a*, Longitudinal section through the head of a small, pigmented, worker-like form; *b*, Longitudinal section through the head of a soldier nymph. The development of the frontal gland and the presence of an outer chitinous sheath indicates that this specimen was soon to molt into a mature soldier; *b*, brain; *con.*, connective; *f.b.*, fat body; *f. gan.*, frontal ganglion; *f.gan.n.*, frontal ganglion nerve; *f.gl.*, frontal gland; *f.gl.d.*, frontal gland duct; *hypoph.*, hypopharynx; *labium.*, labium; *labr.*, labrum; *m.md.*, *m.* adductor mandibulae; *m.med.lab.*, *m.* retractor labri medialis; *m.f.gl.*, muscle of the frontal gland; *n.*, nose; *oes.*, oesophagus; *p.c.*, posterior clypeus; *p.gan.*, posterior ganglion of the oesophageal sympathetic system; *sal.gl.*, salivary gland; *s. gan.*, suboesophageal ganglion; *tent.*, tentorium.

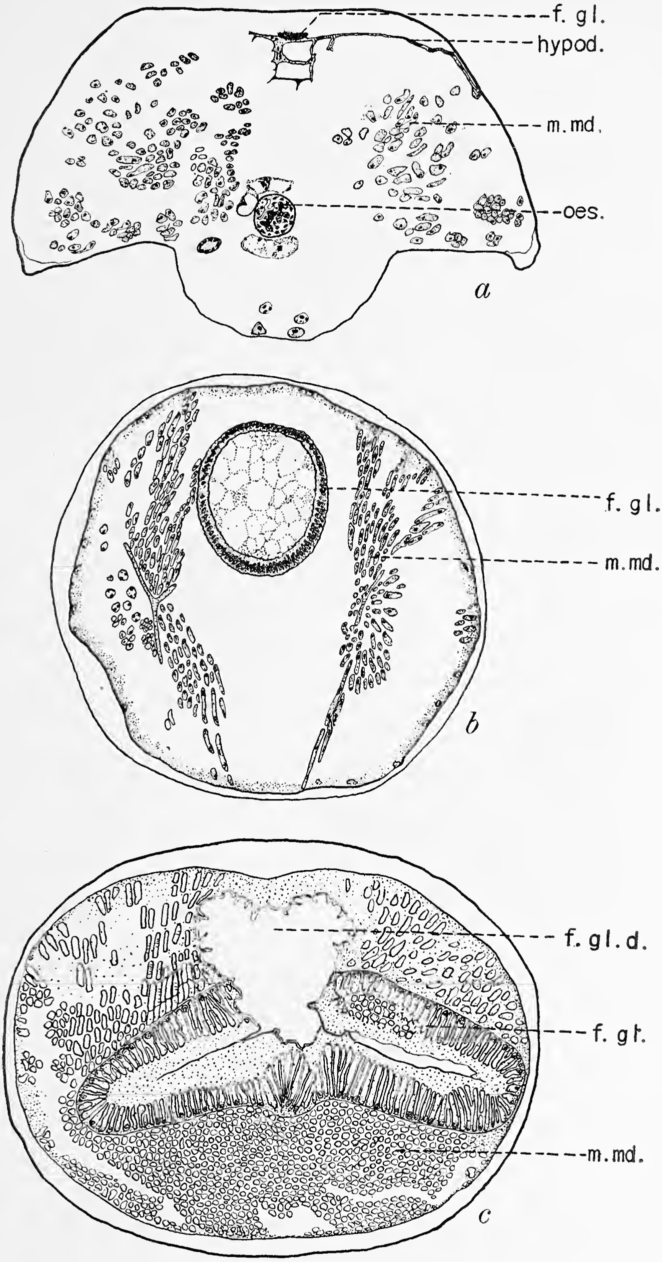


Fig. 32. *a*, Cros-section through the head of a small, pigmented, worker-like form in the region of the frontal gland; *b*, cross-section through the head of a recently emerged soldier nymph in the region of the frontal gland; *c*, cross-section through the head of a mature pigmented soldier in the region of the frontal gland; *f.gl.*, frontal gland; *f.gl.d.*, frontal gland duct; *hypod.* hypodermis; *m. md.*, *m.* adductor mandibulae; *oes.*, oesophagus.

At first I was unable to detect any external difference between the adult workers and the forms which were to molt into soldiers. However, upon careful measurement of head widths of 100 workers and worker-like forms, I found that I could distinguish two groups which never overlapped, one large headed group with head widths from .936 mm. to 1.032 mm. and one small headed group with head widths from .839 mm. to .887 mm. These were further seen to vary slightly in the appearance of the fontanelle, or plate marking the opening of the frontal gland. The smaller type had a somewhat larger and more distinct fontanelle than the larger type. Upon careful measurement, I found that all the molting individuals were coming from the skins of the smaller of the two types. I therefore assume, although it is admitted that the number of molting forms is not enough to be certain, that the soldier develops from the smaller of the two types of pigmented workers. Sections of these types also show a slight difference in the development of the frontal gland, the smaller form having the larger gland. In both cases, however, the gland is very small and difficult to find in the sections and may be considered to be in an embryonic, non-functional state.

The small worker-like form (Fig. 24) differs considerably from the mature soldier (Fig. 25) however. The pigmentation is almost the same in these forms and also in the mature worker. The head of the soldier is prolonged into a "nose" through which a duct (Fig. 31, *b*) runs for the purpose of conducting the fluid secreted by the frontal gland to the surface. The mandibles of the soldier (Fig. 28, *b*) are rudimentary and non-functional. The antennae of the soldier (Fig. 25) are longer than those of the worker-like form (Fig. 24) and consist of 15 segments instead of 16 as found in the worker-like form. Other differences which are not so apparent will be discussed under the changes which take place during the molting.

No frontal process is present in the worker-like form (Fig. 27, *a*) and the mandibles (Fig. 28, *a*) are toothed and functional, being used for cutting wood. They resemble those of the imago in appearance. At the time of molting the individual becomes inactive, lies on its side with its head bent down, and does not move. The integument splits along the Y-suture in the head (Fig. 27, *b*), and along the dorsal side of the thorax and the first few abdominal segments (Fig. 26). The nose starts to grow out (Fig. 27, *b*) until it gets quite long (Fig. 27, *c*). As the skin is shed the emerging individual assumes the shape of the solider nymph.

The soldier nymph emerging from the worker-like skin is white, the posterior portion of the head is not enlarged as it is in the mature soldier (Fig. 27, *d*), the nose is stouter and the frontal gland (Fig. 32) is not yet fully developed. I feel certain, although I found no specimens molting from this stage to the mature soldier type, that there is yet another molt before the final form is reached. Of the many soldier nymphs observed with the developed nose, all were of this shape or else were of the exact type of the mature soldier except that they lacked pigmentation to a considerable extent. No intermediate types were found which would have been the case had the nymph, emerging from the worker-like stage, assumed the shape of the mature soldier gradually without another molt. The soldier nymph illustrated in Fig. 31, *b* shows the stage just before the final molt.

The mature soldier (Fig. 27, *d*) is quite different in shape from the nymph just described (Fig. 27, *c*). The head bulges in back and a section shows the frontal gland has enormously developed (Fig. 32, *c*). The nose is more slender.

That the frontal gland develops gradually while in the stage of the soldier nymph is apparent from the longitudinal section of one of these nymphs (Fig. 31, *b*) which shows a more highly developed gland than that shown in cross-section (Fig. 32, *b*), although the two specimens were alike in external appearance.

The antennae, mandibles, maxillae and labium of the soldier nymph as it emerges from the worker-like skin, are essentially the same as those of the mature soldier except that they are not chitinized and are not as compact as their final form (Fig. 28, *b;* Fig. 29, *b;* Fig. 30, *b*).

It is interesting to note that one segment of the antenna is lost during this process. In all other cases of which I am aware, the antennae, if anything, add segments during the molt. In this case, I believe that the third and fourth antennal segments of the worker-like form fuse into one.

In addition the segments of the antennae become longer and, correlated with this, the maxillary palpi and labial palpi become much elongated (Figs. 29–30).

A summary of these changes follows:

1. The head prolongs itself into a long "nose" from a flat surface, the end of the nose corresponding to the fontanelle plate in position at the junction of the Y-suture (Fig. 27, *a–b*).

2. The antennae each lose one segment, probably through the fusion of the 3d and 4th segments of the worker-like form, and in addition the antennal segments elongate.
3. The mandibles change from large toothed types to reduced non-functional small points (Fig. 28).
4. The maxillae lose the hairy end of the galea and the palpi become much elongated (Fig. 29).
5. The labium changes in shape, the submentum growing longer side projections and the palpi elongating (Fig. 30).

Internally other changes take place.

6. The frontal gland develops from a small inconspicuous organ composed of modified hypodermis (Fig. 32, *a*) into a large sac rounded in outline (Fig. 32, *b*) and later, in the soldier nymph, it becomes further differentiated with two side lobes (Fig. 32, *c*).
7. A duct develops from the hypodermis running to the end of the nose which, in the mature soldier, is hard and ridged on the inside (Fig. 31, *b;* Fig. 32, *c*).
8. The frontal gland muscle (Fig. 31, *b*) enlarges and becomes functional. I have not seen this muscle in sections of the workers and worker-like forms, but Holmgren (1909) illustrates it in the head of an imago of *Nasutitermes*.
9. The muscle situated medially from above the brain to the labrum, *the m. retractor labri medialis* (Fig. 31), becomes very much reduced in the soldier.
10. The *m. adductor mandibulae,* becomes more compact and probably becomes non-functional (Figs. 31–32).

Social Significance of the Facts Presented

The facts outlined seem to indicate that this termite has a specialized, worker-like soldier nymph which functions as a worker in the colony. The contents of the intestines of these worker-like forms indicated that they gathered sand and wood in no way different from the actions of the mature worker. At different times I observed both types of workers carrying sand to their nest and in the nest both seemed to function alike in the care of the queen and other members of the colony.

After passing through this pigmented, functional worker stage, they again become soft, unpigmented and dependent upon the other forms for food. After passing through the unpigmented,

nasuate soldier nymph stage and again molting, the same individual assumes the function of defense in the colony with the use of the now functional frontal gland secretion. The soldier is now unable to feed itself or to carry on any of the specialized activities of its former life.

Is not this change nearly as remarkable as that found in the insects with complete metamorphosis?

The only parallel case I know among termites is that of the nymphs of the reproductive and soldier castes of the *Kalotermitidae.* Here we find nymphs again carrying on the worker functions and later, as far as is known, molting and developing into soldiers or reproductive forms. We are reasonably sure that there is no worker caste among the *Termopsinae, Stolotermitinae* and *Kalotermitinae* (Imms, 1919; Thompson, 1919, 1922).

Phylogenetic Development of Castes

Little is known of the phylogenetic origin of the termite castes, nor do we know any facts that might lead to an explanation of their occurrence such as determining factors in the chromosomes. We are not even sure whether they have developed after the origin of social life or whether something analogous to the castes might not have existed before, such as we find in the wingless and winged states of certain Homoptera, Heteroptera and Zoraptera. No fossils exist which might be of assistance in solving this problem, so we are forced to draw our conclusions from the linear series presented by living termites.

Many biologists have found the evolution of polymorphism among social insects fertile ground for speculation. I believe that a brief historical review will serve to focus our attention upon the significance of the facts known and thus cause greater activity in the search for new facts.

Darwin (1859) in the 'Origin of Species' states:

"The subject well deserves to be discussed at great length, but I will here take only a single case, that of working or sterile ants. How the workers have been rendered sterile is a difficulty; but not much greater than that of any other modification of structure. . . . But I must pass over the preliminary difficulty. The great difficulty lies in the working ants differing widely from both the males and the fertile females in structure, as in the shape of the thorax, and in being destitute of wings and sometimes of eyes, and in instinct. . . . According to M. Verlot, some varieties of the double annual stock from having been long

and carefully selected to the right degree, always produce a large proportion of seedlings bearing double and quite sterile plants. These latter, by which alone the variety can be propagated, may be compared with the fertile and female ants, and the double sterile plants with the neuters of the same community. As with the varieties of the stock, so with social insects, selection has been applied to the family, and not to the individual, for the sake of gaining a serviceable end."

Weisman also held this view of the phylogenetic origin of termite castes (1893, 1894). In a later book (1909), he makes the following statement:

"If we regard the variation of the many determinants concerned in the transformation of the female into the sterile worker as having come about through the gradual transformation of the ids into worker-ids, we shall see that the germ plasm of the sexual ants must contain three kinds of ids, male, female, and worker-ids, or, if the workers have diverged into soldiers and nest-builders, then four kinds. We understand that the worker-ids arose because their determinants struck out a useful path of variation, whether upwards or downwards, and that they continued in this path until the highest attainable degree of utility of the parts determined was reached. But, in addition to the organs of positive or negative selection-value, there were some which were indifferent, as far as the success, and especially the functional capacity of the workers, was concerned; wings, ovarian tubes, *receptaculum seminis*, a number of the facets of the eye, perhaps even the whole eye. As to the ovarian tubes it is possible that their degeneration was an advantage for the workers in saving energy, and if so, selection would favour the degeneration; but how could the presence of eyes diminish the usefulness of the workers of the colony? or the minute *receptaculum seminis*, or even the wings? These parts have therefore degenerated because they were of no further value to the insect. But if selection did not influence the setting aside of these parts because they were neither of advantage or disadvantage to the species, then the Darwinian factor of selection is here confronted with a puzzle which it cannot solve alone, but which at once becomes clear when germinal selection is added. For the determinants of organs that have no further value for the organism, must, as we have already explained, embark on a gradual course of retrograde development."

Wheeler (1917) makes the following statement:

"In most species of ants the constant and striking structural differences between the different castes would, at first sight, suggest that such forms as the apterous females, apterous males, soldiers and workers, must have arisen as so many saltatory variations, or mutants and that they survived and secured representation in the germ-plasm, because they happened to fulfill specialized and useful functions in the life of the colony. I believe, however, that this view of the castes, at least so far as their origin is concerned, cannot be maintained, because all the available evidence points to their being merely the surviving extremes of graduated and continuous series of forms, the annectant members of which have suffered phylogenetic suppression or extinction."

Thompson (1917) in commenting upon the phylogenetic origin of termite castes makes the following statement:

"The manner in which these castes have arisen in the individual life cycle is perhaps indicative of the way they arose phylogenetically. The phylogeny of *Leucotermes* may have begun in a primitive ancestral reproductive type with a tendency to throw off sterile or worker variations, perhaps mutants. This tendency became fixed in the species, and the generalized reproductive type and the generalized worker-soldier type occurred side by side in every generation. Both types still kept the tendency to vary, or mutate; as time went on, the generalized reproductive type threw off the more specialized adults of the second form, with short wing pads, etc., the type itself continuing as the adult of the first form, with ancestral structure and habits. If the third reproductive caste, with no wing pads, is a true caste, it may be accounted for, according to this hypothesis, as a second mutant from the ancestral parent reproductive type. . . . Still later, the generalized worker-soldier type differentiated or split up into the highly specialized soldier caste and the primitive worker caste which more nearly resembles the parent form. Both soldier and worker may manifest their inherent variability by occasional fertility."

Imms (1919) discusses the phylogenetic development of the castes at some length and offers many interesting theories to explain the facts. Following are quotations from this important contribution:

"Certain phases of polymorphism among social insects appear to me to admit of a relatively simple interpretation in terms of the Mendelian theory of heredity. In the present instance it is not my intention to attempt to explain the phenomenon in any insects other than the Termitidae. Among the Hymenoptera it is an attribute of the female sex, and has apparently evolved along somewhat different lines. According to the usually accepted biological criteria, the characters of the ancestral type among the Termitidae are exhibited, in their least modified form, in the winged males and females. The soldiers betray obvious specialisations on the one hand, and indications of degeneration on the other. For this reason it is probable that the primitive Termites consisted solely of winged males and females, and exhibited at first no manifestations of a communal life. The prototype of the worker can be explained as having risen as a mutation of the nymph stage, and characterised by the absence of wing rudiments, and the possession of a markedly larger head and jaws than those of the race from which it sprang. Natural selection would then come into play and favour the increased development of useful characters, and the degeneration of certain others, along lines already suggested by Weismann (*loc. cit.*). It is probable that the soldier caste similarly arose by a further mutation or series of mutations. The fact that transitional forms, intermediate in character between the soldier, worker, and winged castes, are practically unknown argues in favour of these mutations being inherited according to the laws of Mendelian segregation. . . .

The presence of worker-like individuals in *Archotermopsis* has a direct bearing upon the origin of the worker castes among Termites. . . . I consider that they exhibit the first step in the evolution of the worker caste, a conclusion which, if correct, is in full accordance with the presence of other primitive features associated with *Archotermopsis*. At the same time they afford a clue as to the possible origin of the worker, which appears to have arisen as a mutation of the nymphal stage and not of the winged adult. . . .

. . . . In its general morphological features the worker is clearly a less modified form than the soldier. Whether the former is phylogenetically the older type or not is uncertain. . . . At present, . . . we have insufficient evidence to decide whether the soldier mutation arose *de novo* from the nymphal form, or secondarily as a further offshoot from the worker."

Imms makes an attempt to compose a genetic formula on the basis of several allelomorphs expressing themselves collectively in the winged sexual adults and includes the further development of polymorphism among the sterile castes in the explanation.

I do not find it possible to make Imms' genetic formula agree with known facts. He postulates the mating of two heterozygous winged sexual forms which results in the many combinations of factors which might determine the various castes. Among the progeny, however, appear homozygous winged sexual forms which if mated together would produce nothing but homozygous winged sexual forms. This hardly conforms to the known biological observations on termites. It might, however, still be possible to construct a theoretical genetic formula with the introduction of lethal factors. Snyder (1925) has suggested the presence of lethal factors.

On the basis of these admitted speculations, Imms arrives at the following conclusions:

"The Mendelian inheritance of mutations offers a possible solution of polymorphism among Termites, and more especially affords an explanation of: (1) The absence of intermediate forms between the castes; (2) the constant occurrence in each generation of castes which themselves have become sterile; (3) the occurrence of dimorphism and trimorphism among workers and soldiers; (4) the occasional presence of wing rudiments in members of sterile castes, and the occurrence of 'nymph-soldiers' and 'nymph-workers'."

Snyder (1920) summarizes his paper on 'The colonizing Reproductive Adults of Termites' as follows:

"It seems to the writer not unreasonable to conclude that the second and third reproductive forms, as well as the intermediates, in termites are mutations. They, so far as is known, breed true to type; in this case, then, all castes are mutations from the parent first form, and a plausible explanation for the phenomenon of polymorphism is afforded."

Thompson's (1922) posthumous paper on the castes of *Termopsis* contains at the end a discussion of the theory of the origin of polymorphism from which the following quotations are taken:

"Thompson and Snyder (1919), attempting to answer the question of the mode of origin of the termite castes, suggested that the castes might be interpreted either as a series of fluctuating variations or as mutations "comparable to the series of mutations found in *Drosophila*." To-day, the writer, influenced by the recent work of Morgan and his school, especially by their interpretation of the genetic behavior of *Oenothera lamarckiana*, believes that termite castes should be interpreted as comparable to the offspring of *Oenothera*, as arising by segregation from a heterozygous parent form. In modern terminology, therefore, the termite castes are not mutants, in the sense of the progeny of *Drosophila*, arising once for all from a mutating parent, and then breeding true, but are rather segregants, in the sense of the offspring of *Oenothera lamarckiana*, arising generation after generation by splitting and recombination of the genes of a heterozygous parent form. My views on this point therefore, are in general agreement with those of Imms, except in the use of the term mutant, which cannot to-day be applied with exactness to the recurrent termite castes.

With another theoretical point advanced by Imms I am unable to agree. . . . Imms' statement, that workers may have arisen as mutations of the nymphal stage, and not of the winged adult, has a flavor of the neoteinic or 'substitution' idea, which seems in disharmony with his other views and which I am unable to support."

Whether these castes have arisen by fluctuating variations, mutations, or as segregants still remains a matter for speculation. However, we may gain insight into the courses along which the castes have developed phylogenetically by a study of the polymorphism found in living termites.

It seems obvious that at least the second form reproductive type originated phylogenetically from the first form because of the presence of wing buds, compound eyes, and ocelli. Whether the third form originated from the first form, second form or worker, is not quite so obvious. As the workers are sterile and are lacking in groups that possess the third form, however, it is probable that the origin of this caste lies in the first or second form.

As far as is known, the *Termopsinae, Stolotermitinae* and *Kalotermitinae* lack workers, but possess well developed soldiers and the three reproductive castes. References to workers in these groups are probably all erroneous as indicated by the careful work of Thompson (1917, 1919, 1922), Imms (1919) and others. A true adult worker caste may, however, be present in *Mastotermes* and *Hodotermes.* These two genera, however, are socially more highly special-

ized than the *Termopsinae, Stolotermitinae,* and *Kalotermitinae,* and if, after careful investigation, an adult worker caste is found to be present, it is conceivable that it has been developed phylogenetically in a different manner from the worker of the *Rhinotermitidae* and *Termitidae.* The worker caste would thus be polyphyletic. Otherwise, one must assume that the worker caste in the *Termopsinae, Stolotermitinae* and *Kalotermitinae* has been lost secondarily. This latter view is held by Claude Fuller, but the evidence to support it or refute it is very meager. The presence of a true worker caste in the most primitive termites would indicate that this caste had been secondarily lost in the higher forms.

Although *Mastotermes* is generally considered the most primitive termite from a morphological standpoint, its social life is by no means as primitive as that found in various genera of the *Kalotermitidae* (*Archotermopsis, Termopsis, Kalotermes*) and even in morphological characteristics, *Archotermopsis* is more primitive in some respects. Imms (1919) makes the following statement:

> "*Mastotermes* is remarkable in that it possesses a well developed anal lobe in the hind pair of wings, the tarsi have five complete joints, ocelli are present, and sub-anal styles occur in both sexes. These primitive characters are wanting in *Archotermopsis.* On the other hand in the possession of 6–8 jointed cerci, longer sub-anal styles and reniform eyes in the winged forms, the latter genus retains generalized features which are not found in *Mastotermes.* These two genera are to be regarded as divergent offshoots from the primitive Isopteran stock."

An additional primitive character in *Archotermopsis* not found in *Mastotermes* is the presence of compound eyes in the soldier. *Archotermopsis* also lacks the worker caste. With regard to this point Imms (1919) says:

> "During a tolerably intimate acquaintance with this species in India for nearly two years, I never came across any true workers, and no evidence is forthcoming proving that such a caste exists."

Even if a true worker exists in *Mastotermes,* a point which needs careful verification, it would be difficult to believe that this caste had been lost secondarily in *Archotermopsis* which shows certain more generalized features than *Mastotermes.*

I hold the opinion that the soldier caste has developed phylogenetically from the first form reproductive adult and not from the worker as suggested by Thompson (1917). The evidence for my opinion is found in the following facts:

1. Primitive soldiers are sometimes fertile or approach fertility (Heath, 1903; Imms, 1919; Thompson, 1922).
2. Soldiers are often found with wing buds which may be pigmented in the *Kalotermitidae.* None with wing buds have ever been found in the higher termites, however. If the soldiers evolved from the third form, how could they possess wing buds?
3. The primitive soldiers always possess small compound eyes and may even possess traces of the lateral ocelli in some cases.
4. Soldiers are found among all the primitive termites, even where the worker is lacking. The only genus which lacks soldiers (*Anoplotermes*) has obviously lost them secondarily as all its close relatives possess soldiers.

It has previously been thought (Snyder, Banks & Snyder, 1920) that the soldiers are probably specialized workers. Miss Thompson has also stated in her correspondence with me that "the worker is evidently more primitive (phylogenetically) than the soldier." These views are probably the result of the accepted views on the phylogenetic origin of the soldier caste in the true ants. In the *Formicidae* the soldier is undoubtedly a specialized worker and is absent in the primitive ponerine ants.

Now the question arises as to the origin of the worker. Did it arise from the nymphs of the reproductive types as found in the *Kalotermitinae* as suggested by Imms (1919)? I believe the evidence points in another way.

In the first place, Thompson (1917, 1919) finds two types of nymphs at the time of hatching, the sterile prototype and the fertile prototype. This even extends to the *Kalotermitidae* concerning which she (1919) makes the following statement:

> "In size, shape and general external appearance these newly hatched nymphs (*Calotermes* n.sp.) are all alike, but, as in the genus *Reticulitermes,* they are separable by means of internal structures into two types: (a) nymphs with a large brain that almost fills the cavity of the head, large sex organs, and a white dense abdomen, the reproductive or fertile type; and (b) nymphs with a smaller brain that does not nearly fill the head cavity, smaller sex organs, and a transparent abdomen, the soldier (the worker caste is lacking in the genus *Calotermes*), or sterile type."

These same results are obtained from the study of *Termopsis, Cryptotermes,* and *Neotermes,* all belonging to the *Kalotermitidae.* In the higher termites (*Rhinotermitidae* and *Termitidae*) the sterile type and reproductive type are still found, but the sterile type not only develops into soldiers, but also into workers. This fact in-

dicates that the worker has not arisen phylogenetically from the reproductive castes, at least in the *Rhinotermitidae* and *Termitidae,* but is more closely related to the soldier.

Thompson and Snyder (1920) point out close morphological similarities between the third form reproductive type and the worker, but considerations in the following paragraphs seem to preclude the possibility of the worker originating from the third form reproductive caste.

The worker also shows no characteristics which link it to the reproductive castes that are not also possessed by the soldier at some stage in its development. No thoroughly verified case of fertile workers or workers with wing buds has ever been described. Silvestri (1901) says he found a number of workers of *Termes* (=*Microcerotermes*) *strunckii* with well developed reproductive organs. A careful anatomical study would be necessary before the exact caste of these individuals could be thoroughly established, however.

Further evidence of the close relationship of the workers and soldiers is seen in the development of *Nasutitermes* (*Constrictotermes*) *cavifrons* described in the preceding pages, where a soldier of one of the most highly specialized living termites passes through a worker stage which is even socially functional. If the worker has originated phylogenetically from any of the reproductive types, this ontogenetic development of the soldier would be very difficult to explain providing we accept the conclusion expressed in the preceding pages that the soldier is the most primitive sterile caste.

If the soldier is the more primitive of the sterile castes, as the facts lead me to believe, and if the worker has not developed from any of the reproductive castes, the only conclusion left for us to make is that the worker has developed from the soldier caste. The facts lead me to further qualify this statement by saying that the worker is probably a mature caste which seems to have developed phylogenetically through the specialization of soldier nymphs before they had attained the development of the mandibles and head which is characteristic of the mature soldier. This accounts for the fact that the workers resemble the imago more closely in their mouth parts and shape of head than they do the mature soldier. The young soldiers in the early stages of their development also resemble the imago in these respects.

Before this theory of the phylogenetic origin of the worker caste can be applied to all termites, careful investigations of the

development of the worker caste in *Mastotermes* and *Hodotermes* must be completed.

The two sterile castes, workers and soldiers, after their establishment in the phylogenetic series, have further differentiated, the workers dividing in some cases (*Syntermes, Bellicositermes, Nasutitermes, Microcerotermes*) into two or more types which are mature as far as we know. The soldiers have evolved other types such as the minor soldier of *Rhinotermes, Bellicositermes, Acanthotermes,* etc., and also the nasuate soldier has developed from the mandibulate type through intermediate stages such as *Syntermes, Cornitermes* and *Armitermes* and after attaining the nasuate type, has still further differentiated into as many as three mature types found in *Diversitermes.* The soldier of *Constrictotermes* may conceivably have developed from one of these three soldier types, the other two, including the primitive nasuate soldier type, having been eliminated during the course of evolution.

The view that the nasuate soldier is not a true soldier but is a separate caste (nasutus) suggested by Thompson and Snyder (1919) and Imms (1919) has found its way into some recent text-books but has no facts to support it. Snyder, in a recent paper, refers to the "nasutus" as a soldier and points out the significance of the form found in the genus *Armitermes* which is intermediate between the mandibulate and the nasuate soldier.

To my mind, the most remarkable case of phylogenetic differentiation among the sterile castes of termites is found in the genus *Rhinotermes,* s.str. *Schedorhinotermes* possesses an intermediate stage in the development described below.

The facts indicate that the large mandibulate soldier of *Rhinotermes* gave rise to a minor soldier which gradually developed an elongated labrum for dispersal of the secretion of the frontal gland, and lost the large mandibles which gradually degenerated into functionless minute points. This evolution finally resulted in the establishment of two types of soldiers within the same colony, one specialized for biting, the other specialized for the emission of a defensive volatile liquid.

How could such an evolution take place when the soldier cannot reproduce and thus pass on useful variations or mutations to succeeding generations? Is it theoretically possible for one sterile caste to give rise to another in the phylogenetic series as many facts reviewed in the preceding pages seems to indicate has happened?

In order that natural selection may have influenced this evolution, it is necessary for us to assume that the parents that produce the best adapted sterile castes survive and pass on to their fertile progeny the power to produce the same types of sterile castes.

As the sterile caste must originate in the germ plasm of the fertile caste, the statement that one sterile caste originates phylogenetically from another must be modified somewhat. The set of determiners in the germ plasm which cause the production of one sterile caste would have to evolve another set of modified determiners during the course of evolution so that the original sterile caste, such as the major soldier (having itself undergone evolution), and a somewhat different sterile caste, such as the minor soldier, could be produced by the same fertile pair. This fertile pair would also possess other sets of fertile and sterile caste determiners that would produce all the other castes. If such a conception is true, when we referred to the phylogenetic development of one caste from another, we would mean that the set of determiners in the fertile forms that produced the new caste would have evolved from the set of determiners in the fertile forms that produced the more primitive caste.

Thompson (1922) disagrees with Imms' (1919) conception that one caste could evolve from the nymph of another. In my opinion there is no greater difficulty in this theory than in the theory that one highly specialized larva of, let us say, the Tricoptera could evolve from a more generalized larva or that the adult female glow-worm (*Phengodes*) could have evolved by specialization of the larva stage.

These speculations, I hope, will serve to point out the importance of further investigations of the ontogenetic and phylogenetic development of the castes of social insects, particularly cytological, genetic, and embryological studies which at present are almost wholly lacking.

Summary and Conclusions

1. A nasuate soldier nymph was found emerging from a pigmented worker-like skin.
2. Two types of fully pigmented workers can be distinguished by head measurement in the colony, the smaller of which internally shows a slightly more developed frontal gland than the larger type.
3. Both types function in the colony as workers and their food is the same.

4. The smaller of these worker types develops into the soldier and during the metamorphosis, the head is prolonged into a 'nose,' the number of antennal segments is reduced from 16 to 15, the mandibles become degenerate and functionless, the maxillary and labial palpi elongate and also the antennae segments elongate, the frontal gland enlarges into a conspicuous sac, a duct develops from the hypodermis connecting the frontal gland with the end of the 'nose' and, finally, new muscles are developed while other muscles become smaller.
5. Food does not seem to have any possible influence upon the development of the soldier at this stage.
6. The 2d form reproductive type has probably arisen phylogenetically from the 1st form reproductive type.
7. The soldiers have probably arisen phylogenetically from the 1st form reproductive type and may be considered the primitive sterile caste.
8. The workers of the *Rhinotermitidae* and *Termitidae* have probably arisen phylogenetically from the soldier nymphs which have not yet attained the specialized shape of the head and mandibles found in mature soldiers.
9. Both the sterile castes have further differentiated phylogenetically into other types, some of which have attained a high degree of specialization along other lines from the original sterile type. Two or three different types of soldiers and two or three different types of workers may be found in the same colony.
10. Speculations on the mechanism of phylogenetic and ontogenetic development of the castes of social insects serve to point out great gaps in our knowledge of this phenomenon.

BIBLIOGRAPHY

Banks, N. and Snyder, T. E.
1920. A Revision of the Nearctic Termites. Bull. 108, U. S. National Museum, pp. 1–228.

Bobe-Moreau.
1843. Mémoire sur les termites observés à Rochefort.

Bugnion, E.
1912. Observations sur les termites Différenciation des castes. Comp. Rend. soc. biol. Paris. I, t. 72, pp. 1091–1094.
1912a. *Eutermes lacustris* nov. sp. de Ceylan. Revue Suisse Zool. vol. 20, pp. 487–505.

1913. Observations sur les termites. Bull. soc. ent. France, No. 8.
1913a. Le *Termes horni* Wasm. de Ceylan. Revue Suisse Zool. vol. 21, pp. 299–330.
1913b. Les Termites de Ceylan. Le globe, Geneve, vol. 52, pp. 24–58.
1913c. La différenciation des castes chez les Termites. Bull. Soc. Ent. France, 1913, pp. 213–218.
1914. La Biologie des Termites de Ceylan. Bull. Mus. Hist. nat. Paris, No. 4, pp. 170–204.

CLEVELAND, L. R.
1923. Correlation between the Food and Morphology of Termites and the Presence of Intestinal Protozoa. Am. Journ. Hygiene, vol. 3, pp. 444–461.
1923a. Symbiosis between Termites and their Intestinal Protozoa. Proc. Nat. Acad. Sci., vol. 9, pp. 424–428.
1924. The Physiological and Symbiotic Relationships between the Intestinal Protozoa of Termites and their Host, with special Reference to *Reticulitermes flavipes* Kollar. Biol. Bull., vol. 46, pp. 177–225.
1925. The Ability of Termites to live perhaps indefinitely on a diet of pure Cellulose. Biol. Bull., vol. 48, pp. 289–293.
1925a. The Feeding Habit of Termite Castes and its Relation to their Intestinal Flagellates. Biol. Bull., vol. 48, pp. 295–308.
1925b. The Effects of Oxygenation and Starvation on the Symbiosis between the Termite, *Termopsis*, and its Intestinal Flagellates. Biol. Bull., vol. 48, pp. 309–326.

DARWIN, CHARLES.
1859. Origin of Species, Chap. 8.

DESNEUX, J.
1904. Genera Insectorum de P. Wytsman, fasc. 25. Isoptera. Bruxelles. 52 pp.

DEWITZ, H.
1878. Beiträge sur postembryonalen Gliedmassenbildung bei den Insecten. Zeitsch. wiss. Zool., Bd. 30, Suppl.

EMERY, C.
1893. Zusammensetzung und Entstehung der Termitengesellschaften. Biol. Centralbl., Bd. 13, pp. 758–766.
1894. Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen. Biol. Centralbl., Bd. 14.
1896. Le polymorphisme des fourmis et la castration alimentaire. Comp. Ren. des. Séances du 3me Congrès intérnat. de Zool., Leyden.
1904. Sur Kenntniss des Polymorphismus der Ameisen. Zool. Jahrb., Suppl. 7.
1910. Il polimorfismo e la fondazione delle Società negli insetti sociali. Scienta, Rivista di Scienza, vol. 7, no. 14–2.

ESCHERICH, K.
1909. Die Termiten oder weissen Ameisen. Leipzig. 198 pp.

FEYTAUD, J.
1912. Contribution a l'étude du Termite lucifuge. Arch. d'anat. micros., t. 13, pp. 481–607.

GRASSI, B. AND SANDIAS, A.
1893–94. Costituzione e sviluppo della Società dei Termitidae. Atti Acad. Gioenia di sci. nat., Catania, vol. 6, pp. 1–75, vol. 7, pp. 1–76.
1896–97. The Constitution and Development of the Society of Termites; Observations on their habits; with Appendices on the parasitic Protozoa and on the Embiidae. Translated by W. F. H. Blandford. Quart. Journ. Micros. Sci., vols. 39–40.

HAGEN, H.
1855–60. Monographie der Termiten. Linn. Ent., vol. 10, 12, 14.

HEATH, H.
1903. The Habits of California termites. Biol. Bull., vol. 4, pp. 44–63.

HOLMGREN, W.
1909. Termitenstudien. I. Anatomische Untersuchungen. K. Svenska Vet.-Acad. Handl., Bd. 44, No. 3, 215 pp.

IMMS., A. D.
1919. On the structure and biology of *Archotermopsis*, together with descriptions of new species of intestinal protozoa and general observations on the Isoptera. Philos. Trans. Royal Soc. London., Ser. B, vol. 209, pp. 75–180.

JUCCI, C.
1920. Sulla differenziazione della caste nello Societa dei Termitidi i neotenici. I. Rend. del. R. Accad. Nazionale dei Lincei, (Anno CCCXVII) vol. 29, 30, ser. 5, 20, sem. fasc. 10–20.
1924. Su la differenziazione de le caste ne la Societa dei Termitidi. Reale Accad. Nazionale dei Lincei, (Anno CCCXX, 1923) vol. 14, ser. 5, fasc. 9.
1925. Il problema dei reali veri del *Reticulitermes lucifugus*. Bol. Soc. Ent. Ital. anno 57, n. 7, Lugio 31.

KNOWER, H.
1894. Origin of the 'Nasutus' of *Eutermes*. Johns Hopkins Univ. Circ., vol. 13, pp. 58–59.

LESPÈS, C.
1856. Recherches sur l'organisation et des moeurs du Termite lucifuge. Ann. Soc. Nat. Zool., 4 ser., t. 5, pp. 227–282.

MJÖBERG, E.
1920. Results of Dr. E. Mjöbergs Swedish Scientific Expeditions to Australia 1910–1913: Isoptera. Ark. f. Zoologi, Bd. 12, No. 15, pp. 1–128.

MÜLLER, F.
1873–75. Beiträge zur Kenntniss der Termiten. Jen. Zeitsch. Naturwiss, Bd. 7.

SILVESTRI, F.
1901. Operai ginecoidi di Termes con osservazioni intorno l'origine delle varie caste nei Termitidi. R. Acc. Lincei, vol. 10, pp. 479–484.
1902. Ergebnisse biologischen Studien an sudamerikanschen Termiten. Allg. Zeitschr. Entom., Bd. 7, no. 9, pp. 173–178, 257–260, 289–293, 326–334.
1903. Contribuzione alla Conoscenza dei Termitidi e Termitofili dell' America meridionale. Redia, vol. 1, pp. 1–234.

SNYDER, T. E.
1913. Changes during the quiescent stages in the metamorphosis of termites. Science, vol. 38, pp. 487–488. Also Proc. Ent. Soc. Washington, vol. 15, pp. 162–165.
1915. Biology of the Termites of the eastern United States, with preventative and remedial measures. U. S. Dept. Agric., Bur. Ent., Bull. no. 94, pt. II, pp. 13–85.
1916. Termites, or 'white ants,' in the United States; their damage, and methods of prevention. U. S. Dept. Agric., Bur. Ent. Prof. Paper, Bull. 333.
1920. The Colonizing Reproductive Adults of Termites. Proc. Entom. Soc. Washington, vol. 22, pp. 109–150.
1925. The Origin of the Castes in Termites. Proc. Biol. Soc. Washington, vol. 38, pp. 57–68.

SPENCER, HERBERT.
1893–94. The inadequacy of 'Natural Selection.' Contemp. Rev. vol. 63, pp. 153–166, 439–456, 743–760; vol. 64, pp. 893–912.

THOMPSON, C. B.
1916. The Brain and the Frontal Gland of the Castes of the 'White Ant,' *Leucotermes flavipes*, Kollar. Journ. Comp. Neurology, vol. 26, pp. 553–603.
1917. Origin of the Castes of the Common Termite, *Leucotermes flavipes* Kol. Journ. Morph., vol. 30, pp. 83–153.
1919. The Development of the Castes of Nine Genera and Thirteen Species of Termites. Biol. Bull., vol. 36, pp. 379–398.
1922. The Castes of *Termopsis*. Journ. Morphology, vol. 36, pp. 495–535.

THOMPSON, C. B. AND SNYDER, T. E.
1919. The Question of the Phylogenetic Origin of Termite Castes. Biol. Bull., vol. 36, pp. 115–132.
1920. The 'Third Form,' the Wingless Reproductive Type of Termites: *Reticulitermes* and *Prorhinotermes*. Journ. Morph., vol. 34, pp. 591–633.

WEISMANN, A.
1892. Das Keimplasma. Eine Theorie der Vererbung. Jena.
1893. The all-sufficiency of natural selection. Contemp. Rev., vol. 63, pp. 309–338.
1894. The effect of external influences upon development. Romanes Lecture, London.
1902. Vorträge über Descendenz-theorie. Jena.
1909. The Selection Theory: in 'Darwin and Modern Science.' Edited by Seward, pp. 29–37.

WHEELER, W. M.
1907. The polymorphism of ants, with an account of some singular abnormalities due to parasitism. Bull. Amer. Mus. Nat. Hist., vol. 23, pp. 1–93.
1910. Ants, their structure, development and behavior. New York.
1917. The Phylogenetic Development of Subapterous and Apterous Castes in the Formicidae. Proc. Nat. Acad. Sci., vol. 3.

New York Zoological Society

OBJECTS OF THE SOCIETY

A Public Zoological Park. A Public Aquarium. The Preservation of our Native Animals. The Promotion of Zoology.

ZOOLOGICA VOL. I

		Paper	Cloth
Parts 1–20	*Not bound*	3.85	
Parts 1–20	*Bound*		6.00

Postage-weight, 4 pounds

Zoologica Vols. I, II and III completed and indexed.
Subjects in Vol. I furnished on application, see address 4th page of cover.

ZOOLOGICA VOL. II

1—Two Series of Amphibians (*Deckert*)	.25
2—Tetrapteryx Stage, Ancestry Birds (*Beebe*)	.25
3-4—Notes, Birds, Para, Brazil; Fauna of Jungle Debris (*Beebe*)	.25
5—The Gaff-Topsail Catfish (*Gudger*)	.25
6—Mammals of Australia in the Zoological Park (*W. H. D. Le Souef*)	.75
7-8-9—Vertebrates, British Guiana (*Beebe*)	.25
10—Habits of Sage Grouse (*Horsfall*)	.25
11—Eclipse Plumage, Domestic Fowl (*Crandall*)	.25
12—Life History of the Puffer (*Welsh-Breder*)	.25
13—Hermaphroditism of the Croaker (*Breder*)	.25
14—Food of Certain Minnows (*Breder-Crawford*)	.25
15—Fishes of Sandy Hook Bay (*Breder*)	.25
16—Weaving of Weaver Birds (*Friedman*)	.25
17—Scales of Whitefishes (*Mellen-Van Oosten*)	.30
18—The Anderson Tree Frog (*Noble*)	.25

Postage, Zoologica, 5 cents

ZOOLOGICA VOL. III

	Paper	Cloth
1-2—Objects, Tropical Research Station (*Osborn*)	.25	
Contributions Tropical Research Station (*Beebe*)		
3-11—Social Beetles, British Guiana (*Wheeler*)		
Tachigalia Ants (*Wheeler*)		
Habits of Cucujidae (*Wheeler*)		
New Coleoptera (*Schwarz-Barber*)		
Larvae, Pupae, Social Beetles (*Boving*)		
New Diadiplosis (*Felt*)		
New Blepyrus (*Brues*)		
Tachigalia Membracids (*Herbert Osborn*)		
New Entomobrya (*Folson*)	1.00	
12—Fetuses, Guiana Howling Monkey (*Schultz*)	.50	
13—Mammals Collected Tropical Research Sta. (*Anthony*)	.25	
14-15—New Batrachians (*Noble*). New Lizards (*Noble*)	.25	
16—Descriptiones Termitum in Anglorum Guiana Reportorum (*Silvestri*)		
17—New Genera and Species, Termitophilous Coleoptera (*Mann*)		
18—Glandular Structure, Abdominal Appendages, Termite Guest (*McIndoo*)		
19—Termitophilous Apterygota (*Folsom*)		
20—Three Apparently New Species, Termitaphis (*Morrison*)		

	Paper	Cloth
21—Termitophilous Millipeds (*Chamberlin*)	.75	
22-23—A Termitophilous Braconid (*Brues*). Two Myrmecophilous Phoridae (*Brues*)	.25	

Postage, Zoologica, 5 cents

ZOOLOGICA VOL. IV

1—Fishes, Amphibians, Reptiles (*Breder*)	.15	
2—Frozen Mammoths (*Lang*)	.25	
3—Galapagos Tortoises (*Townsend*)	.50	
4—Some Panama Fishes (*Breder*)	.20	
5—Locomotion of Fishes (*Breder*)	1.25	

ZOOLOGICA VOL. V

1—Williams Galapagos Expedition (*Beebe*)	.15	
2—Galapagos Heterocera (*Schaus*)	.20	
3—Galapagos Lepidoptera (*Beebe*)	.15	
4-16—Ichthyology (*Nichols*)		
Apterygota (*Folsom*)		
Homoptera (*Osborn*)		
Mallophaga (*Ewing*)		
Diptera (*Johnston*)		
Arachnida (*Banks*)		
Formicidae (*Wheeler*)		
Triungulin Larvae (*Brues*)		
Chilopods (*Chamberlin*)		
Coccidae (*Morrison*)		
Brachyuran Crabs (*Rathbun*)		
Macrura and Anomura (*Schmitt*)		
Hymenoptera (*Rohwer*)	.50	
17—Neuroptera (*Banks*)	.15	
18—Isopods (*Van Name*)	.25	
19—Copepods (*Wilson*)	.15	
20—Coleoptera (*Mutchler*)	.20	
21—Hemiptera-Heteroptera (*Barber*)	.15	

ZOOLOGICA VOL. VI

1—Ecology of Kartabo (*Beebe*)	1.00	
2—Birds of Kartabo (*Beebe*)	.35	
3—Membracidae of Kartabo (*Haviland*)	.30	
4—Termites of Kartabo (*Emerson*)	1.00	
5—Ispods of Kartabo (*Van Name*)	.30	

ZOOLOGICA VOL. VII

1—Three-Toed Sloth (*Beebe*)	.60	
2—Development of Soldier Termites (*Emerson*)		
3—A New Polychaetous Annelid (*Treadwell*)		

ZOOLOGICA VOL. VIII

1—The Arcturus Expedition (*Beebe*)		
2—Arcturus: Equipment and Operation (*Tee-Van*)		
3—Brotulid Fishes (*Trotter*)		
4—Galapagos Brachyura (*Boone*)		

ZOOLOGICA VOL. IX

1—Marine Fishes—New York and So. New England (*Nichols-Breder*)		

Publications of the Society for sale at the Zoological Park, 185th Street and Southern Boulevard, New York City.

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

DEPARTMENT OF TROPICAL RESEARCH
KARTABO, BRITISH GUIANA

VOLUME VII. NUMBER 3

Department of Tropical Research Contribution Number 245

A NEW POLYCHAETOUS ANNELID

By A. L. Treadwell

PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

November 4, 1926

New York Zoological Society

General Office: *101 Park Avenue,* New York City

Officers

President, MADISON GRANT;
Vice-Presidents, FRANK K. STURGIS; AND HENRY D. WHITON;
Chairman, Executive Committee, MADISON GRANT;
Treasurer, CORNELIUS R. AGNEW.
Secretary, WILLIAM WHITE NILES

Board of Managers

Class of 1927

MADISON GRANT, WM. WHITE NILES, FRANK K. STURGIS, OGDEN MILLS, LEWIS R. MORRIS, ARCHER M. HUNTINGTON, GEORGE D. PRATT, T. COLEMAN DU PONT, HENRY D. WHITON, CORNELIUS R. AGNEW, HARRISON WILLIAMS, MARSHALL FIELD

Class of 1928

PERCY R. PYNE, GEORGE BIRD GRINNELL, CLEVELAND H. DODGE, ANTHONY R. KUSER, MORTIMER L. SCHIFF, FREDERIC C. WALCOTT, GEORGE C. CLARK, JR., W. REDMOND CROSS, HENRY FAIRFIELD OSBORN, JR., ARTHUR A. FOWLER, GEORGE GORDON BATTLE, BAYARD DOMINICK

Class of 1929

HENRY FAIRFIELD OSBORN, LISPENARD STEWART, CHARLES F. DIETERICH GEORGE F. BAKER, ROBERT S. BREWSTER, EDWARD S. HARKNESS, WILLIAM B. OSGOOD FIELD, EDWIN THORNE, JOHN E. BERWIND, IRVING K. TAYLOR, HARRY PAYNE BINGHAM, LANDON K. THORNE

Scientific Staff

W. REID BLAIR, *Director of the Zoological Park;*
CHARLES H. TOWNSEND, *Director of the Aquarium;*
RAYMOND L. DITMARS, *Curator of Mammals and Reptiles;*
WILLIAM BEEBE, *Honorary Curator of Birds and Director of Department of Tropical Research;*
LEE S. CRANDALL, *Curator of Birds;*
GEORGE S. HUNTINGTON, *Prosector;*
H. C. RAVEN, *Associate Prosector;*
CHARLES V. NOBACK, *Veterinarian;*
ELWIN R. SANBORN, *Asst. to Sec'y. and Editor.*

Editorial Committee

MADISON GRANT, *Chairman;*

WILLIAM T. HORNADAY
WILLIAM BEEBE
CHARLES H. TOWNSEND
ELWIN R. SANBORN, Sec'y.

A NEW POLYCHAETOUS ANNELID*
FROM KARTABO, BRITISH GUIANA
Genus *Namonereis*

BY A. L. TREADWELL

(Fig. 33)

A single specimen belonging to this rare genus was collected at Kartabo, British Guiana, and submitted to me for examination through the courtesy of Mr. William Beebe. The specimen lacks the pygidium and is much coiled so that accurate measurements of length are not obtainable. The prostomial width is 1.5 mm. and the greatest body diameter is not over 2 mm.

The prostomium is trapezoidal in outline, its anterior end somewhat narrower than the posterior, (Fig. 33, A). The tentacles are small, broadly lanceolate in outline and situated on the anterior lateral angles of the prostomium, thus separated from one another by almost the entire prostomial width. Owing to imperfect preservation, the surface of the prostomium is very much wrinkled and I am uncertain whether a very narrow transverse band across the anterior margin is an artefact or is really present in the living animal. There is also an indistinct transverse line running across the prostomium just in front of the eyes. The eyes are very large, the two on the same side being partly fused so that under low magnification they appear as one. The proboscis is devoid of paragnaths and the jaws which are dark colored on their outer margins and light on the inner, have eight denticulations. The palps are very heavy and extend to only a short distance in front of the prostomium. The terminal joint of the palp is very small.

Of the tentacular cirri the anterior dorsal is the longest, extending to a distance of one-half its length beyond the apex of the palp. The posterior dorsal one is similar to this in form, but is shorter and the two ventral ones are very short. All have very short cirrophores.

As is common in this genus, the peristomium is short and inconspicuous. Nothing in the coloration of the preserved specimen

*Contribution, New York Zoological Society, Department of Tropical Research No. 245.

merits especial mention. The parapodia have essentially similar forms throughout the body, though in the posterior ones the dorsal cirri are broader than in the anterior. (Fig. 33, B is taken from the fifteenth somite.) The notopodium is rudimentary, being indicated only by the presence of a single acicula which extends into it and it

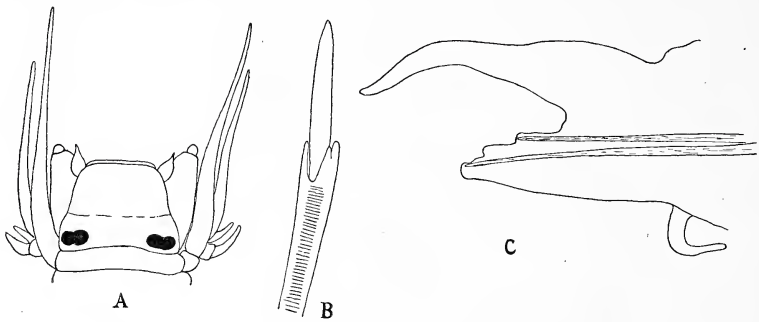


Fig. 33, A.B.C. *Namonereis kartaboensis* Treadwell. sp. nov. A, anterior end of body x 10; B, fifteenth parapodium x 35; C, ventral type of seta x 250.

never has setae. The neuropodium is elongated and somewhat irregularly lobed at the apex, and has a single acicula. The dorsal cirrus is very broad at the base but narrows to an acute apex extending far beyond the setal lobe. The ventral cirrus is very small.

Two types of setae occur in all parapodia. The first type resembles the ordinary nereid setae in that it is compound, the basal joint camerated, the terminal joint elongated, sharp pointed and with a row of denticulations along one edge. The length of the terminal joint is variable. The second type of seta is quite unusual in form in that while it is compound with a camerated basal portion, the terminal portion is blunt pointed and without any trace of denticulations, (Fig. 33, C). The setae of the first type resemble one form described by Gravier in *N*(*Lycastis*) *ouanaryensis* (1901 page 356, figure 3), while the other is somewhat like Gravier's figure 4, but does not have the row of spike-like processes near the base. In general the setae of the first type lie in the dorsal part of the seta-tuft, those of the second in the ventral, but there is a certain amount of overlapping in the middle.

Savigny (1820), gave the generic name *Lycastis* to a new species *L. armillaris*, but this specimen was later shown to belong to the genus *Syllis* and is recorded as *S. armillaris*. Audouin and Milne-

Edwards (1832–34 page 199) adopted the generic name *Lycastis* for a nereid and considered that the type species *L. brevicornis,* is intermediate in character between the Nereidae and the Syllidae. Up to the present time, eight species of this genus have been described, one from West Africa, one from Hawaii, one from the west coast of France, two from Brazil, two from French Guiana and one from Chili. The genus is of especial interest, because in contrast to other nereids which are marine it frequently occurs in fresh or brackish water, and Gravier (1901 pages 354–366, 1901a pages 373–379), and Johnson (1903, pages 214–220) have described the structure and ecology of several of the species. Chamberlin (1919 page 196) shows that in accordance with taxonomic rules, *Lycastis* should be reserved for syllids and proposes instead the generic name *Namonereis* with *N. quadraticeps.* Blanchard, as the type. This procedure I have adopted.

Grube (1871 pages 47, 48) described *Namonereis* (*Lycastis*) *abiuma* from Brazil. I have been unable to get Grube's paper and know it only from the summary given by Gravier (1901 pages 374, 375). This species seems to be more nearly related to *N. kartaboensis* than any previously described species but differs in that the anterior dorsal cirri in *N.* (*L.*) *abiuma* are rudimentary while in *N. kartaboensis* they are fully developed from the first. Fauvel however (1923 page 39), records specimens of *N.* (*L.*) *ouanaryensis* Gravier, from French Guiana in which some individuals have rudimentary dorsal cirri in anterior somites while in others they are of normal size, indicating that this feature may be variable. In other respects, such as the character of the posterior dorsal cirri and the arrangement of the eyes, *N. kartaboensis* seems to differ decidedly from *N.* (*L.*) *abiuma.*

BIBLIOGRAPHY.

Audouin J. V. et Milne-Edwards, A.
1834. Recherches pour servir a l'histoire du littoral de la France. Annélides. Paris. t. 2 pp. 1–290, Pls. 1–8.

Chamberlin, R. V.
1919. The Annelida Polychaeta. Memoirs Mus. Comp. Zool. XLVIII, pp. 1–514, Pls. i-lxxx; Reports on U. S. F. C. S. Albatross Expeditions to West Coasts, Mexico, Central and South America, Galapagos Islands, 1891, No. XXXVIII; Tropical Pacific, 1889–1900, No. XX: Eastern Tropical Pacific, 1904–1905, No. XXXI.

FAUVEL, PIERRE
1923. Annélides Polychètes des iles Gambier et de la Guyane. Mem. della Pontificia Academia Romana dei Nuovi Lincei, Ser. 11, Vol. VI, pp. 1–59.

GRAVIER, CH.
1901. Sur trois nouveaux Polychètes d'eau douce de la Guyana francaise. Societe d'histoire naturelle d'Autun. Bull. 14, pp. 353–371.
1901a. Sur le genre Lycastis. Ibid. pp. 373–379.

GRUBE, ED.
1871. Ueber die Gattung Lycastis und ein Paar neuer Arten derselben. Jahresbericht der schles. Gesellschaft fur Vater. Cultur, pp. 48–48.

JOHNSON, H. P.
1903. Fresh water Nereids from the Pacific Coast and Hawaii with Remarks on Fresh-water Polychaetes in general. Mark Anniversary Volume. Art. X, pp. 205–224, Pls. XVI–XVII.

SAVIGNY, J. C.
1820. Système des Annélides principalement des celles de cotes de l'Egypt et de la Syrie.

New York Zoological Society

OBJECTS OF THE SOCIETY

A Public Zoological Park. A Public Aquarium. The Preservation of our Native Animals. The Promotion of Zoology.

ZOOLOGICA VOL. I

		Paper	Cloth
Parts 1–20	*Not bound*	3.85	
Parts 1–20	*Bound*		6.00

Postage-weight, 4 pounds

Zoologica Vols. I, II and III completed and indexed.
Subjects in Vol. I furnished on application, see address 4th page of cover.

ZOOLOGICA VOL. II

1—Two Series of Amphibians (*Deckert*)	.25
2—Tetrapteryx Stage, Ancestry Birds (*Beebe*)	.25
3–4—Notes, Birds, Para, Brazil; Fauna of Jungle Debris (*Beebe*)	.25
5—The Gaff-Topsail Catfish (*Gudger*)	.25
6—Mammals of Australia in the Zoological Park (*W. H. D. Le Souef*)	.75
7–8–9—Vertebrates, British Guiana (*Beebe*)	.25
10—Habits of Sage Grouse (*Horsfall*)	.25
11—Eclipse Plumage, Domestic Fowl (*Crandall*)	.25
12—Life History of the Puffer (*Welsh-Breder*)	.25
13—Hermaphroditism of the Croaker (*Breder*)	.25
14—Food of Certain Minnows (*Breder-Crawford*)	.25
15—Fishes of Sandy Hook Bay (*Breder*)	.25
16—Weaving of Weaver Birds (*Friedman*)	.25
17—Scales of Whitefishes (*Mellen-Van Oosten*)	.30
18—The Anderson Tree Frog (*Noble*)	.25

Postage, Zoologica, 5 cents

ZOOLOGICA VOL. III

	Paper	Cloth
1–2—Objects, Tropical Research Station (*Osborn*)	.25	
Contributions Tropical Research Station (*Beebe*)		
3–11—Social Beetles, British Guiana (*Wheeler*)		
Tachigalia Ants (*Wheeler*)		
Habits of Cucujidae (*Wheeler*)		
New Coleoptera (*Schwarz-Barber*)		
Larvae, Pupae, Social Beetles (*Boving*)		
New Diadiplosis (*Felt*)		
New Blepyrus (*Brues*)		
Tachigalia Membracids (*Herbert Osborn*)		
New Entomobrya (*Folson*)	1.00	
12—Fetuses, Guiana Howling Monkey (*Schultz*)	.50	
13—Mammals Collected Tropical Research Sta. (*Anthony*)	.25	
14–15—New Batrachians (*Noble*). New Lizards (*Noble*)	.25	
16—Descriptiones Termitum in Anglorum Guiana Reportorum (*Silvestri*)		
17—New Genera and Species, Termitophilous Coleoptera (*Mann*)		
18—Glandular Structure, Abdominal Appendages, Termite Guest (*McIndoo*)		
19—Termitophilous Apterygota (*Folsom*)		
20—Three Apparently New Species, Termitaphis (*Morrison*)		

	Paper	Cloth
21—Termitophilous Millipeds (*Chamberlin*)	.75	
22–23—A Termitophilous Braconid (*Brues*). Two Myrmecophilous Phoridae (*Brues*)	.25	

Postage, Zoologica, 5 cents

ZOOLOGICA VOL. IV

	Paper	Cloth
1—Fishes, Amphibians, Reptiles (*Breder*)	.15	
2—Frozen Mammoths (*Lang*)	.25	
3—Galapagos Tortoises (*Townsend*)	.50	
4—Some Panama Fishes (*Breder*)	.20	
5—Locomotion of Fishes (*Breder*)	1.25	

ZOOLOGICA VOL. V

	Paper	Cloth
1—Williams Galapagos Expedition (*Beebe*)	.15	
2—Galapagos Heterocera (*Schaus*)	.20	
3—Galapagos Lepidoptera (*Beebe*)	.15	
4–16—Ichthyology (*Nichols*)		
Apterygota (*Folsom*)		
Homoptera (*Osborn*)		
Mallophaga (*Ewing*)		
Diptera (*Johnston*)		
Arachnida (*Banks*)		
Formicidae (*Wheeler*)		
Triungulin Larvae (*Brues*)		
Chilopods (*Chamberlin*)		
Coccidae (*Morrison*)		
Brachyuran Crabs (*Rathbun*)		
Macrura and Anomura (*Schmitt*)		
Hymenoptera (*Rohwer*)	.50	
17—Neuroptera (*Banks*)	.15	
18—Isopods (*Van Name*)	.25	
19—Copepods (*Wilson*)	.15	
20—Coleoptera (*Mutchler*)	.20	
21—Hemiptera-Heteroptera (*Barber*)	.15	

ZOOLOGICA VOL. VI

	Paper	Cloth
1—Ecology of Kartabo (*Beebe*)	1.00	
2—Birds of Kartabo (*Beebe*)	.35	
3—Membracidae of Kartabo (*Haviland*)	.30	
4—Termites of Kartabo (*Emerson*)	1.00	
5—Ispods of Kartabo (*Van Name*)	.30	

ZOOLOGICA VOL. VII

	Paper	Cloth
1—Three-Toed Sloth (*Beebe*)	.60	
2—Development of Soldier Termites (*Emerson*)		
3—A New Polychaetous Annelid (*Treadwell*)		

ZOOLOGICA VOL. VIII

	Paper	Cloth
1—The Arcturus Expedition (*Beebe*)		
2—Arcturus: Equipment and Operation (*Tee-Van*)		
3—Brotulid Fishes (*Trotter*)		
4—Galapagos Brachyura (*Boone*)		

ZOOLOGICA VOL. IX

	Paper	Cloth
1—Marine Fishes—New York and So. New England (*Nichols-Breder*)		

Publications of the Society for sale at the Zoological Park, 185th Street and Southern Boulevard, New York City.

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

DEPARTMENT OF TROPICAL RESEARCH
KARTABO, BRITISH GUIANA

VOLUME VII. NUMBER 4

Department of Tropical Research Contribution Number 301

A RIVER DOLPHIN FROM KARTABO

BARTICA DISTRICT, BRITISH GUIANA

BY SAMUEL H. WILLIAMS

PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

December 13, 1928

A RIVER DOLPHIN FROM KARTABO*

BARTICA DISTRICT, BRITISH GUIANA

By Samuel H. Williams

University of Pittsburgh

(Figs. 33–45 incl.)

In the spring of 1925, the author was placed in charge of a party of graduate students, to conduct a series of investigations at Kartabo, Bartica District, British Guiana. The Bartica District is generally considered to be that region within a radius of six miles with Kartabo as the center. The mean position is 58° 42′ West, and 6° 23′ North.

Three mighty rivers flow through the district. Of these, the Essequibo, flowing northeast, and carrying a large portion of the drainage waters from the Savannahs, is the largest, having a width of nearly four miles at Bartica. Its largest tributary is the Mazaruni, which runs over a circuitous path from the west, and joins the Essequibo near Bartica. Six miles above this point, the Mazaruni receives the waters from the treacherous and mysterious Cuyuni river which has its origin somewhere in the Venezuelan forests and flows from the Northwest.

At the junction of the Mazaruni and Cuyuni Rivers, situated on the Southern shore of the latter, and surrounded on three sides by the jungle, stands the Tropical Research Station established in 1916 by William Beebe, under the auspices of The New York Zoological Society.

Through the kindness of Mr. Beebe and The New York Zoological Society, the University of Pittsburgh assumed control of the investigations in the summer of 1924, with Dr. Alfred E. Emerson in charge. It was under the auspices of the University of Pittsburgh that the author undertook to continue the work.

From the date of our arrival at Kartabo, and continuing throughout our tenure there, we observed, almost daily between the hours of twelve noon and two P.M., a school of river dolphins which played, or foraged, in the waters of the Cuyuni just opposite the laboratory.

* Contribution, New York Zoological Society, Department of Tropical Research No. 298.

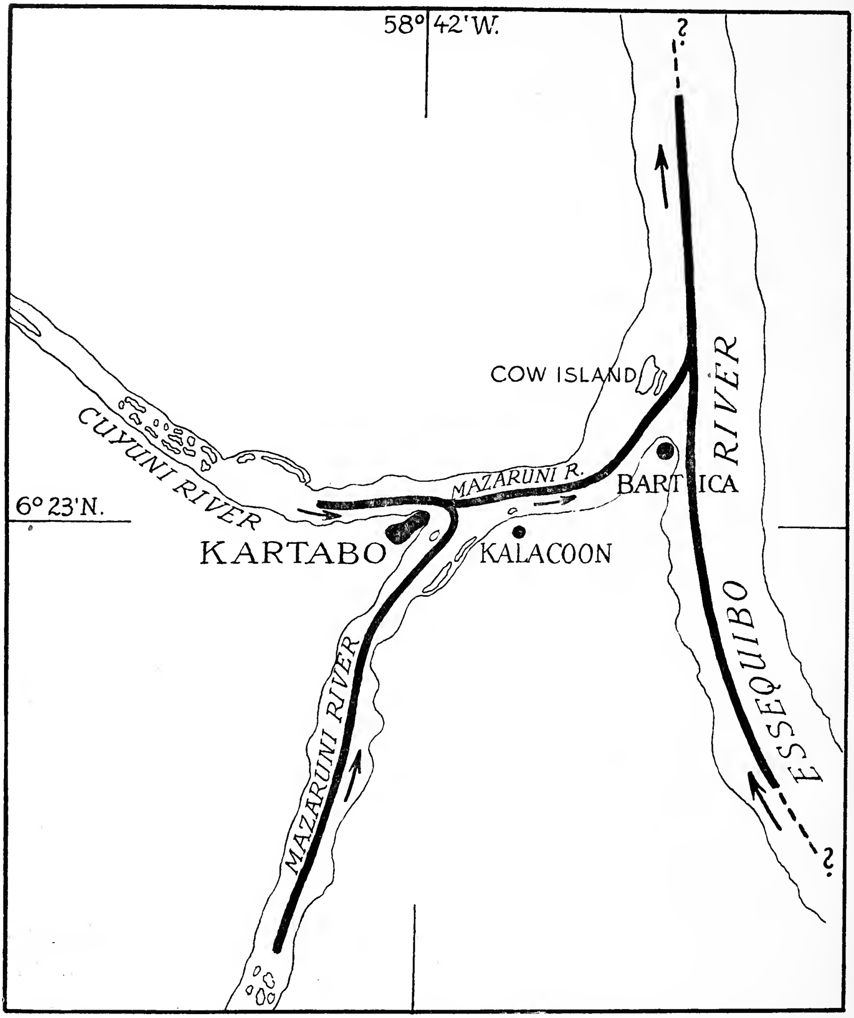


Fig. 34. Sketch map showing the range of activity of *Sotalia guianensis* at Kartabo. Bartica District, British Guiana.

That these animals had been observed for several years prior to this time, is indicated by the fact that Mr. Beebe[1] included them in his list of the mammals of that region. I was later informed by Mr. Beebe that he had seen these animals frequently during the

[1] Beebe: Studies of a Tropical Jungle, etc." Zoologica, Vol. VI, No. 1, 1925. p. 112. In this list Mr. Beebe gives the Genus INIA.

period from 1916 to 1924, but that all attempts to capture specimens were unsuccessful.

On numerous occasions we followed the school which numbered eight specimens. It is interesting to note that all of the animals were apparently mature, and there were no indications of younger forms in attendance. In our endeavors to capture specimens we chased the creatures in canoes equipped with outboard motors but we could not surround them. Harpoons, shot guns, revolvers, and high powered rifles were used without success. Two members of the party registered "hits" and, contrary to our expectations, the animals did not rise to the surface but apparently dived into the mud at the bottom of the river and we did not recover either animal.

It was customary for us to stretch a long gill net in the Cuyuni River each evening. The net was drawn at daybreak. In this way we procured an ample supply of fish for our table.

On the morning of August 11, 1925, when the net was drawn, a specimen was found hopelessly entangled in it. The creature had evidently poked its beak through the strands of the net, and being unable to extricate itself, had drowned.

The animal was immediately subjected to a series of measurements and photographed. The torso was removed and preserved in a fifteen per cent solution of formalin. After removing the skeleton, the skin was placed in a strong solution of salt and alum and the whole was shipped to the University for later study.

The Range of Activity

Observations covering a period of several months, supplemented by informations received from natives, indicated that the range of activity (Fig. 34) of the Cetaceans extended for several miles up and down the three rivers of the District. On frequent occasions the animals were seen to ascend the Cuyuni river for a distance of more than two miles, above Kartabo to Camaria. Further migration in this direction was prevented by a long series of rapids seven miles in extent. At other times we observed the animals in the Mazaruni River in the vicinity of Horaima, which is two miles west of Kartabo. Indians who made frequent fish-shooting expeditions to the rapids several miles further up the river, asserted that they had seen the dolphins near the cataract. At other times, the animals were observed at the mouth of the Mazaruni,

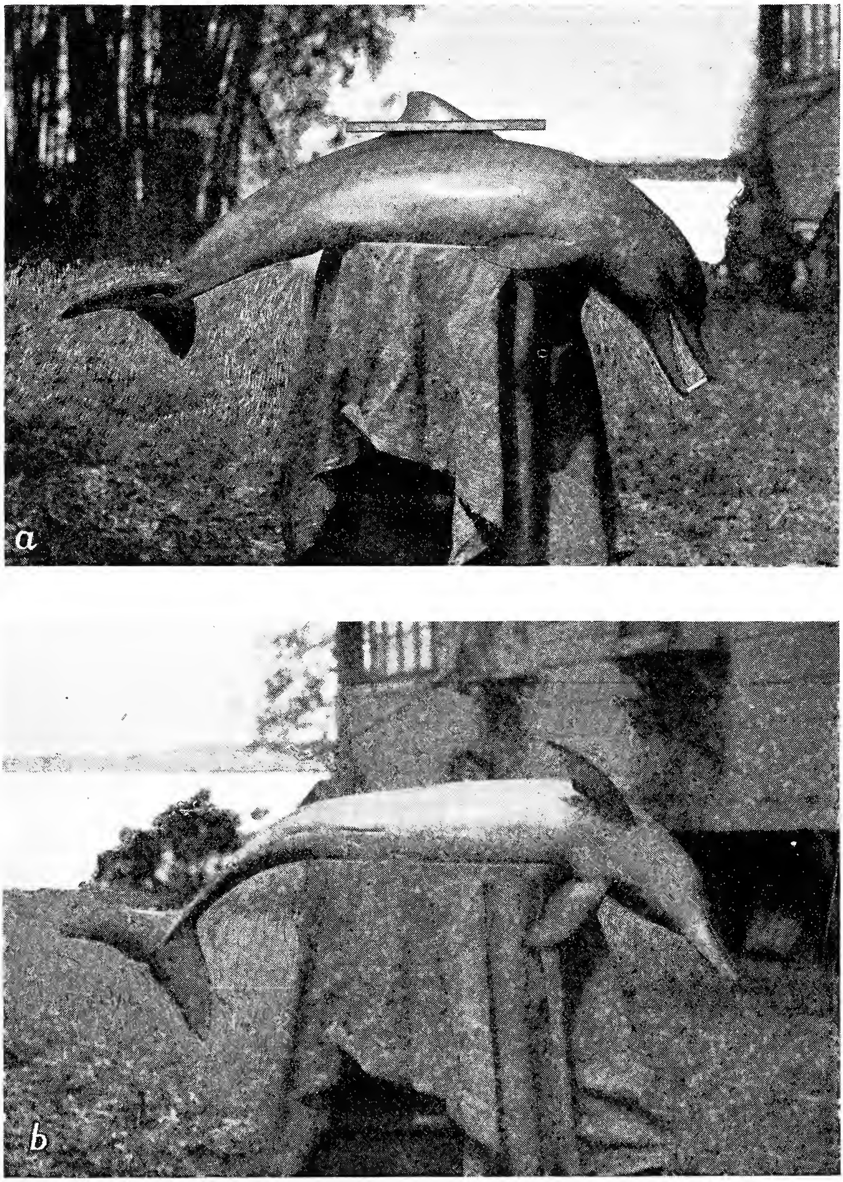


Fig. 35. *a*, *b*, *Sotalia guianaensis* Van Beneden.

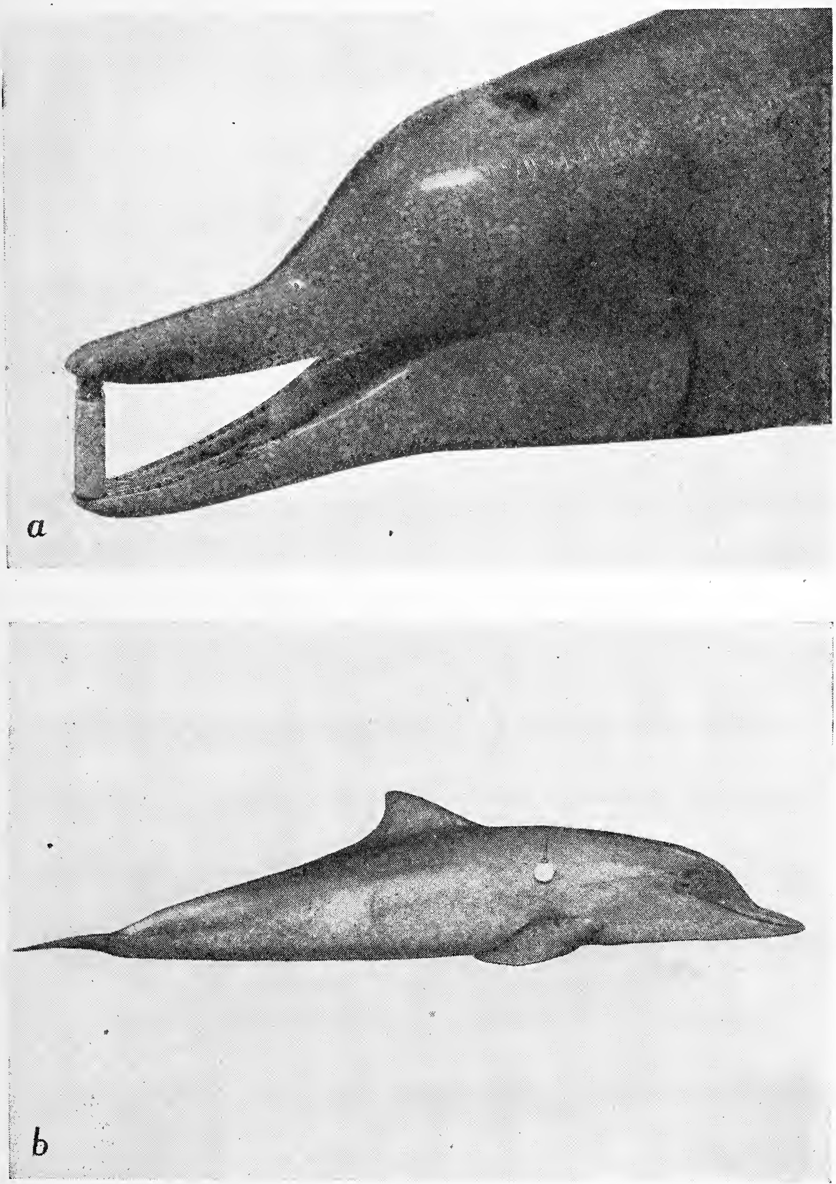


Fig. 36. *a*, *b*, *Sotalia guianensis* Van Beneden.

six miles below Kartabo, by various members of the party. Residents of Bartica reported having infrequently seen them in the Essequibo opposite the village. Bovianders, living eight miles below Cow Island toward the sea coast, also reported the frequent occurrence of the animals at that point.

The animals were never seen above the rapids on any of the three rivers, and information received from Indians, substantiated the conclusion that the rapids were insurmountable barriers to migration.

When informed by Indians living along the Cuyuni river, that they had feasted upon several specimens within the past few months, I accompanied a party of them to their village. After some searching among the refuse around their Benabs, I found the remains of two specimens. The bones had been gnawed by dogs and they were in the last stages of decay. They were, therefore, of no taxonomic value.

They were, however, obviously delphinid remains and from the descriptions in my field notes, they were evidently of the same species as the animal we had secured.

The Specimen—External Characters

The animal, from behind the pectoral fin to the region back of the anus, was of a dull lead color, blending into a pinkish to violet gray along the lateral margins and ventrally (Fig. 37*a*). The pectorals were of the same color as the back.

The external measurements were as follows:

Sex—Male; Locality—Kartabo, British Guiana; Date—August 11, 1925.

Length	5 feet 3¼ inches
Weight	105 pounds
Head—length	11 inches
Mouth—length	8¾ inches
Eye—length	¾ inches
Spiracle (semi circular)—diameter	1 inch
Head girth	24½ inches
Body girth before dorsal fin	29½ inches
Body girth behind dorsal fin	28¼ inches
Caudal girth	9½ inches
Beak	4½ inches
Anus to tip of tail	19 inches
Anus to genital opening	5 inches

Dorsal fin—length 11 inches, height 5 inches
Pectoral fin—length 9¾ inches, width 4¼ inches

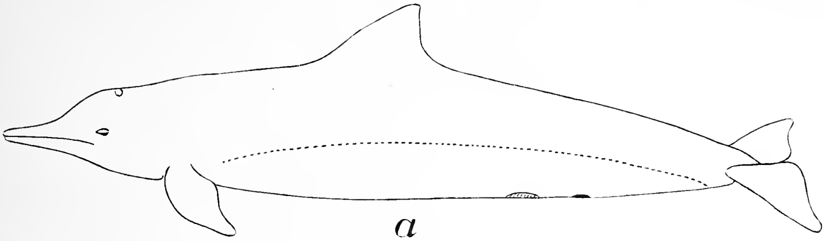


Fig. 37. *a, Sotalia guianensis* Van Beneden. Outline sketch made from field notes

Fig. 37. *b, Sotalia guianensis* Van Beneden; portion of the vertebra showing union of first and second cervicals.

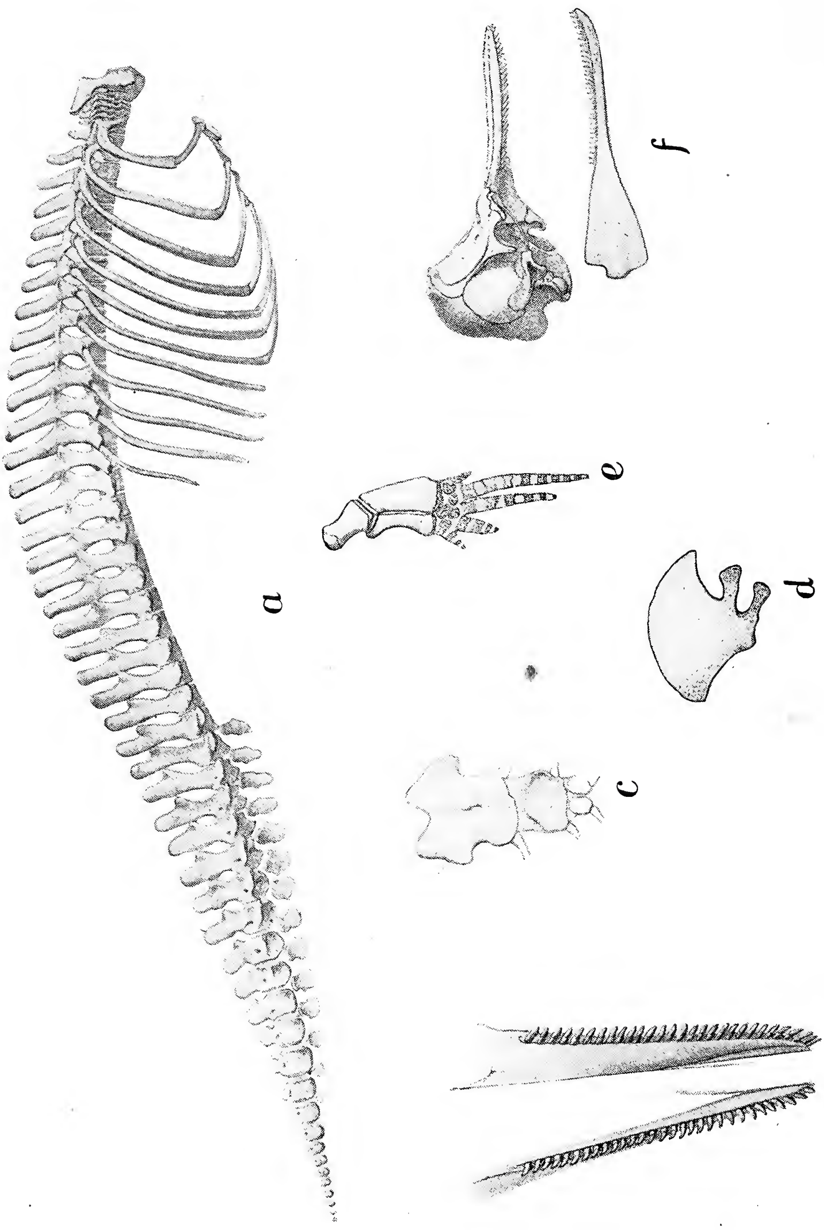


Fig. 38. *a*, *b*, *c*, *d*, *e*, *f*, *Sotalia guianensis* after Van Beneden and Gervais, "Osetographic des Cetaces, vivants at fossils."

Stomach Contents

An examination of the stomach showed it to contain no evidence of Crustacea, although the larger shrimps (*Palaemon amazonicus*) are common. The remains of about thirty-two small herring like fish, and four small cat fish were found. There were also thirty-nine lenses of various sizes, and several otolysts, present. The disintegrated condition of most of the material made the identification of species, virtually impossible.

The Identified Specimen—*Sotalia guianensis* VanBeneden.

A study of the complete skeleton has proved it to be *Sotalia* (*Delphinus*) *guianensis* VanBen. The history and distribution of the genus and species, are worthy of mention. The type was originally described by VanBeneden from a specimen, the locality records of which are somewhat confusing.

A notice of *Delphinus guianensis* appeared in the "Bull. Acad. Royale Belgique, 2e, Ser., Vol. XVI, 1863," but the species was merely indicated as new and no description was given. It was said to have been sent from LaGuyane[2] to the Museum at Stuttgart. The species was definitely introduced as *Delphinus guianensis* in the "Mem. Couron. Acad. Royale Belgique, Coll. in octavo, Tome XVI, 1864." It is here stated that the specimen had been sent from Cayenne, but later on the same page, it is said that the collection containing the animal was from a "Voyageur Naturaliste" in Surinam. VanBeneden at another place "Opusc. Coll. 1857–1887" indicates that the specimen was sent from Cayenne to the Museum at Stuttgart or Würtemburg.

In the "Supplement to the Catalogue of Seals and Whales in The British Museum," 1871, Gray lists *Sotalia guianensis* from British Guiana, and he also states that the specimen is in Stuttgart. In Flower's "List of Cetacea in the Zoological Department of the British Museum," 1885, this record does not appear. True, in "A Review Of the Family Delphinidae," 1889, lists Cayenne as the locality, but he does not refer to the location of the type. Kükenthal, in "Untersuchungen An Walen," 1914, describes the foetus of *Sotalia guianensis* from the Naturalienkabinet at Stuttgart, which was labelled *Steno guianensis*, but he gives no locality record.

VanBeneden and Gervais in "Osteographie des Cetaces, vivants et fossiles, 1880," page 594, state that the descriptions of the genus *Sotalia*, and the species *guianensis*, were made from a specimen taken in Surinam and which was contained in the collection at Stuttgart. However, in the "Explication des Planches" of this work, the figures are stated to have been made from a specimen in the Museum at Louvain. (Fig. 38.)

Sir Sydney F. Harmer, former Director of the British Museum, in reply to my inquiry relative to the locality given by Gray, and to the present location of the type, says "It is not clear to me what is the correct locality. Cayenne may have really been the port of shipment and Surinam is, perhaps, the probable locality. . . 'Gray's Catalogue, 1871, p. 67, mentions *Sotalia guianensis*,' but although he mentions British Guiana as the locality, he does not imply that the species is represented in the British Museum. The locality mentioned by Gray is presumably copied from the 1866 Catalogue, p. 257."

[2] French Guiana.

Dr. M. Rauther, Director of the Würtemburg Naturaliensammlung at Stuttgart, informs me that a skin, skeleton, and foetus of a female specimen of *Sotalia* (*Delphinus*) *guianensis*, are in the collection there (Nr. 1122). The specimen is labelled "Maroni River, Surinam, Kappler, 1865." Dr. Rauther says in part "Es ist leider in unseren altern Zuwachsverzeichnisses nicht vermerkt, ob dass stück Nr. 1122 das origin alexemplar für die Beschreibung VanBeneden ist. Da Sie anscheinend in dem Werke von *VanBeneden*, P. J., & P. Gervais, 'Osteographie des Cetaces recents et fossiles,' Paris, 1868–1877, eine Angabe gefunden haben, wonach das Originialexemplar sich in der Stuttgarter Naturaliensammlung (früher Naturalienkabinet) befände, so ist es immerhin wahrscheinlich dass unser Stück dies Original ist."

True (1889) states that there are at least two specimens of *Sotalia guianensis* in European Museums. He does not indicate, however, that he was aware of their exact locations, and I have been unable to verify the existence of the specimen in Louvain, to which VanBeneden refers.

In order to positively locate the present whereabouts of the type and other specimens, I later wrote to Dr. Rauther, calling his attention to the fact that the species was definitely introduced in 1863, two years prior to the date attached to the specimen. He informed me that they had two specimens of *Sotalia guianensis* at Stuttgart. Both were taken in the Maroni river which separates Cayenne (French Guiana) and Surinam (Dutch Guiana). The locality may, therefore, have been either country. The type specimen (Nr. 1122) was received after its description by VanBeneden. The other specimen had been received earlier and it was the foetus from this that Kükenthal (1914) had described. Dr. Rauther's letter definitely establishes the locality and present location of the type and substantiates my former conclusions. After reviewing the abstract of my investigations Dr. Rauther writes "Nach dem von Ihnen uns freundlicherweise mitgeteilten Auszug aus der *Sotalia guianensis* betreffenden Literatur erscheint es auch mir sicher, dass unser Stück Nr. 1122 als Typus der Species zu gelten hat. Der von *VanBeneden* 1864 gebrauchte Ausdruck "Voyageur Naturaliste" bezieht sich sicherlich auf den Herrn Kappler, der in Niederlandisch—Guyana (Surinam) tätig war und von dort in dem Zeitraum von 1843 bis 1884 reich-haltiges Tiermaterial an unser Museum geliefert hat. Die Jahreszahl 1865 auf der Etikette unserer *Sotalia guianensis* ist vermutlich so zu erklären, dass dieses Stück hier erst in das Zuwachsverzeichnis eingetragen wurde, nachdem es bereits *VanBeneden* zur Bearbeitung vorgelegen hatte; dass sie also nicht das Jahr der Erbeutung, sondern dasjenige ser Aufnahme in unseren Katalog bedeutet. Bei der Durchsicht des zwischen *VanBeneden* un dem damaligen Vorstand unserer Sammlung, *Dr. Krauss*, geführten Briefwechsels fand ich leider nicht mehr auf die Sache Bezügliches, als eine kurze Nachschrift in einem Briefe *VanBeneden* vom 3.7. 1863 (July 3d); "Le Delphin guyana est decrit et fig. dans nos bulletins. Je vous ai envoye un Ex. par Marcus (?) de Bonn. Si vous ne l'avez pas deja, vous le recevrez." Die Fassung der Mitteilung lässt immerhin schliessen, dass das beschriebene Tier *Krauss* bekannt war, also wohl nach Stuttgart gehörte.

Was die Localität der Erbeutung unseres Stücks angeht, so haben wir keinen zwingenden Grund zu zweifeln, dass die Angabe: "Maroni-River" zuverlässig

ist; sie findet sich allerdings nur auf der Etikette, nicht in dem Katalogeintrag. Jener Fluss bildet die Grenze zwischen Niederländisch Guyana und Französich Guyana. Daher erklärt sich wohl das Schwanken der Angaben in der Literatur zwischen "Surinam" und "Cayenne"; es mag sein, dass die Verschiffung von Cayenne aus Stattgefunden hat, wie Sir *Sydney F. Harmer* vermutet.

Das in meinem Briefe vom 19 angeführte "weitere Skelett" trägt übrigens auf der Etikette folgende Bezeichnung: Nr. 533 *Steno guianensis* VanBen. Marowini-Mündung, Surinam, Kappler 1854. Es ist also erheblich früher an unser Museum gekommen, als Haut und Skelett v on Nr. 1122."

Inasmuch as the species is more or less a marine form and not a true river form, it is not unusual or strange that it exists at present in British Guiana which is only about two hundred miles from the location of the type.

The Distribution Of The Genus

The genus *Sotalia* is represented by ten species, two of which are somewhat doubtful.[3] Only three of these are indigenous to South America. *Sotalia tucuxi* Gray, has been taken in the Amazon from Brazil to Peru. A single skull (Cat. no. 21499) in the collections of the United States National Museum, which was purchased from a Biological Supply House, is believed by some writers to be that of *Sotalia tucuxi.* Although there are no records attached to the skull, it is thought to have been originally found in Florida waters.

Sotalia brasiliensis VanBeneden[4] was taken in the Bay at Rio de Janeiro. The specimen was a very young animal and its actual specific characters are still a matter of controversy.

In addition to *Sotalia guianensis* from Surinam and British Guiana, the genus is represented by the following species: *Sotalia perniger* (Elliot) Blyth., from the Indian Ocean, *Sotalia lentiginosus* Owen, from India and Ceylon, *Sotalia plumbea* (Dussumier) Cuvier, also from India and Ceylon, *Sotalia teuszii* Kükenthal, from Camerroun, and *Sotalia sinensis*, Flower, from the China sea and the Foo-Chow and Canton rivers. The two doubtful species are: *Sotalia santonicus* Lesson, from the Atlantic Ocean and *Sotalia maculiventer* Owen, from the Indian Ocean.

Taxonomic Characters

When VanBeneden first described the species he ascribed the name *Delphinus guianensis* to it. However, Gray (1866), in describing certain forms created the genus *Sotalia.* Later (1870) Flower placed the specimen of VanBeneden in this genus because of marked differences between it and the genus *Delphinus* of Linné. The summary of generic characters given by Gray (1866–1871) and by Flower (1870), is as follows: Rostrum long, narrow, and compressed. Symphysis of mandible long or moderate. Pterygoid bones separate, narrow, and divergent posteriorly. Post orbital process of frontal, narrow. Lower jaw rather broad behind, palate flat. Teeth slender, conical, smooth, 26–35.

[3] Trouessart: "Catalogus Mammalium."
[4] Van Beneden: "Mem. Acad. Belg. XLI, 1875."

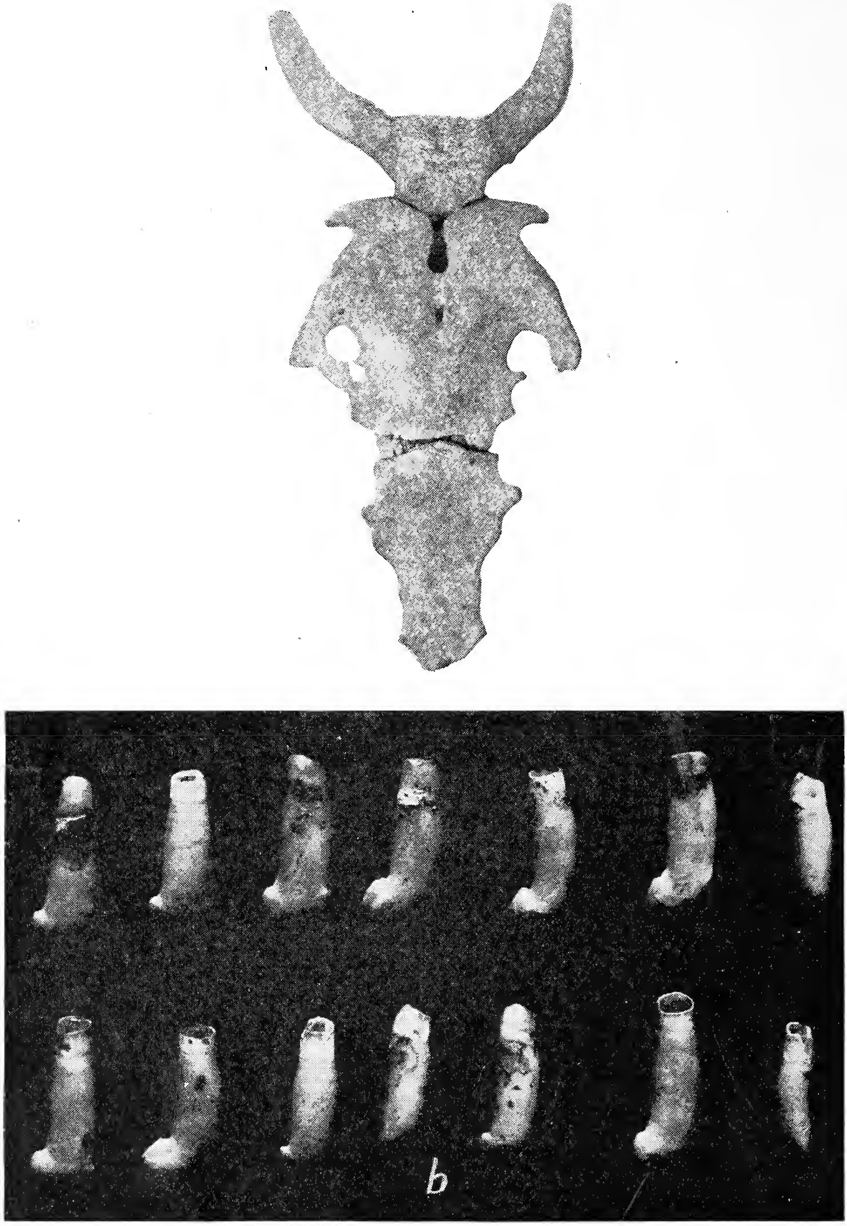


Fig. 39. *a*, *b*, *Sotalia guianensis* Van Beneden; *a*, upper figure sternum; *b*, teeth.

Fig. 40. *Sotalia guianensis* Van Beneden; the rostrum is long, narrow and compressed.

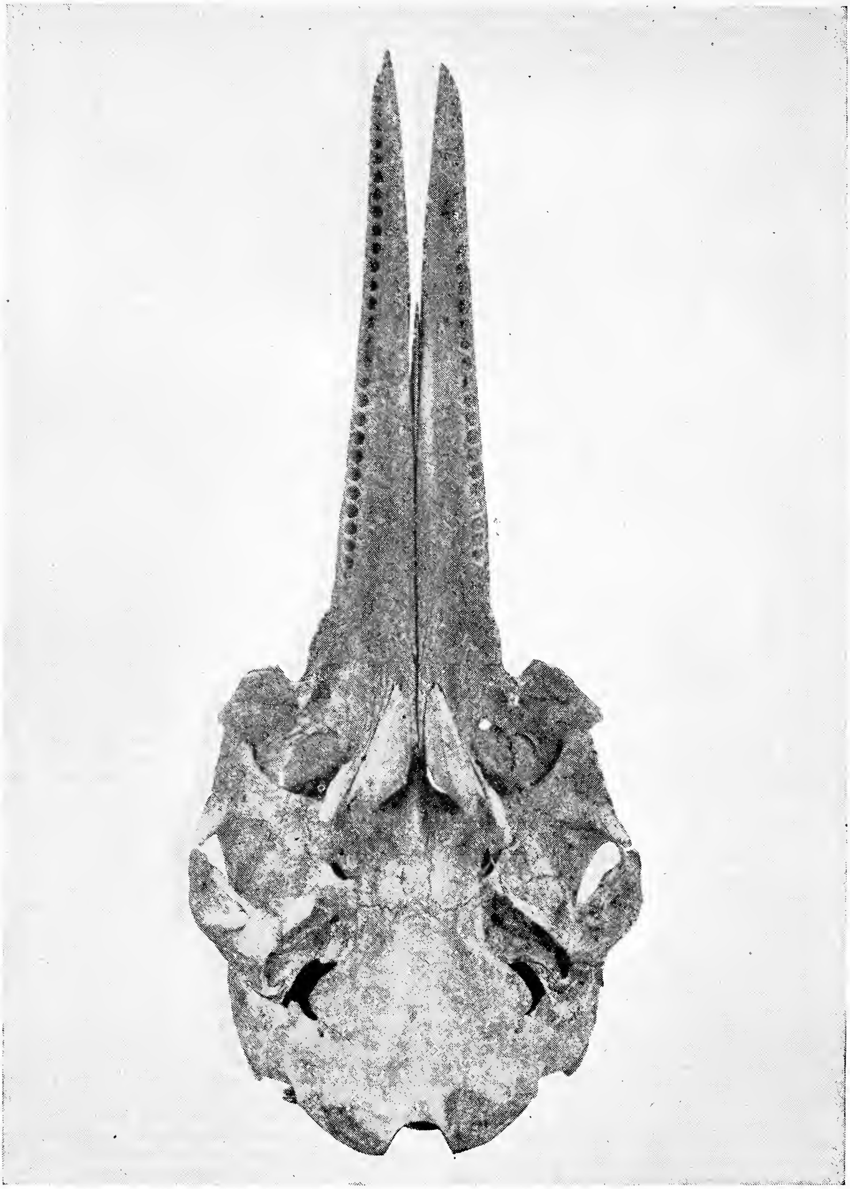


Fig. 41. *Sotalia guianensis* Van Beneden; the pterygoids are separate and divergent posteriorly.

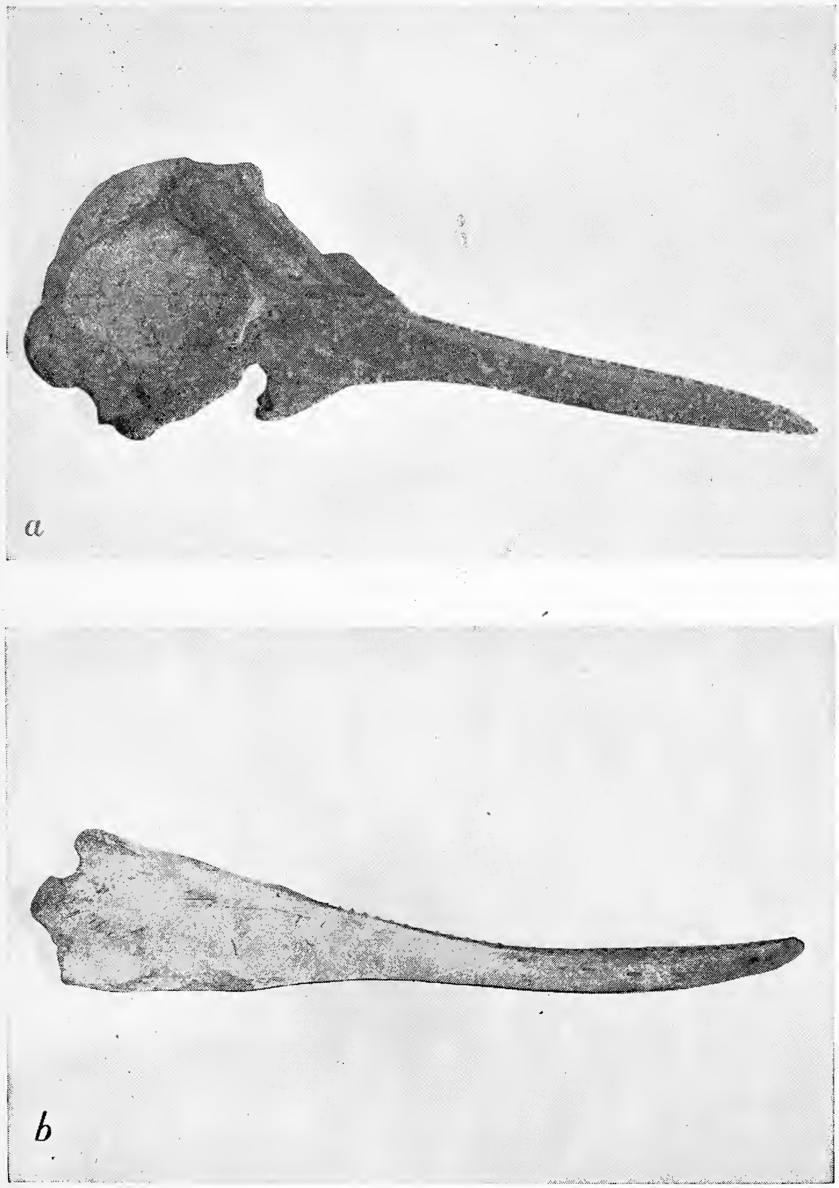


Fig. 42. *a*, *b*, *Sotalia guianensis* Van Beneden; *a*, upper jaw; *b*, lower jaw is high behind and curved.

Fig. 43. *Sotalia guianensis* Van Beneden; the humerus is shorter than forearm and radius is broad.

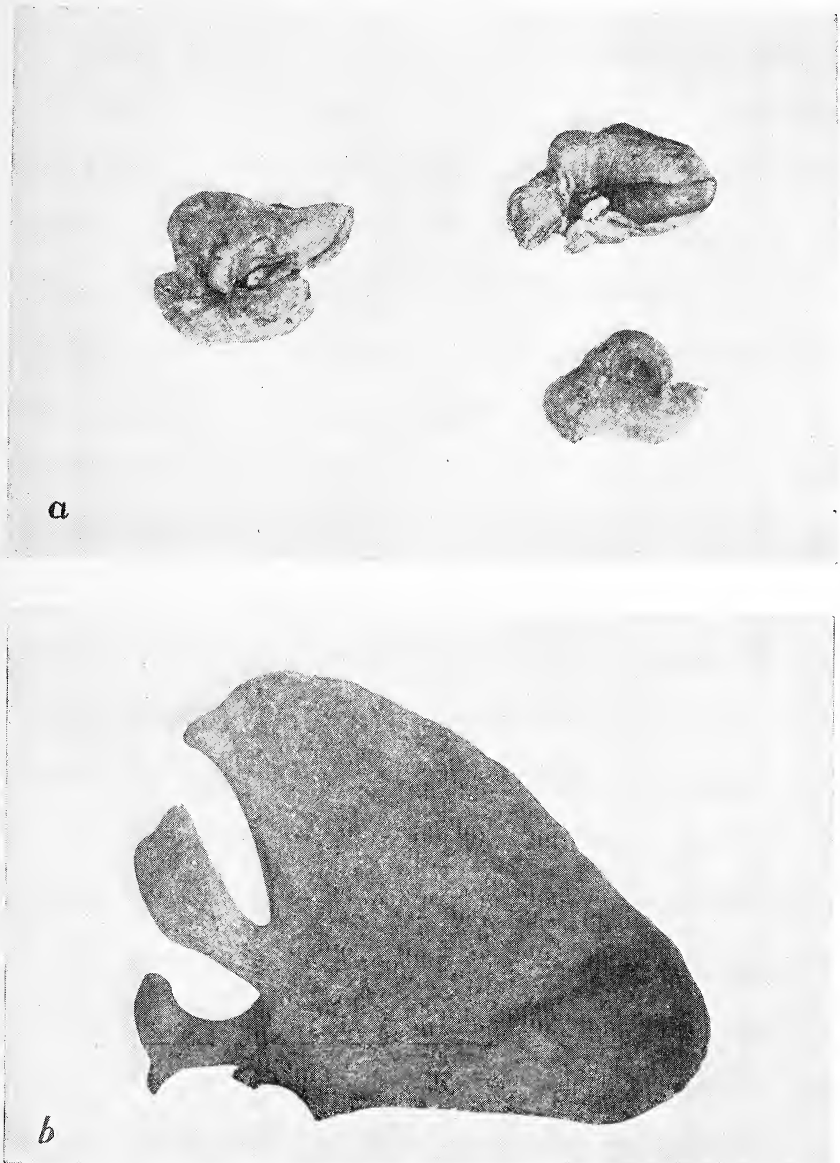


Fig. 44. *a, b, Sotalia guianensis* Van Beneden; *a*, tympanid bones; *b*, the scapula showing the coracoid and acromion.

Vertebra 51–55. Scapula broad, Acromion broad. Dorsal fin falcate, moderate. Color, white or gray, sometimes spotted: no bands of dark color. Scarcely distinct from Steno.

The three chief characters that distinguish the genus *Sotalia* from *Steno* and *Tursiops* are (1) the separation of the pterygoids, (2) the more limited number of caudal vertebrae, and (3) the greater number of teeth. (True—1889.)

The specific characters are, Vertebrae 55: Thoracic 12, lumbar 14, caudal 22, cervical 7. The first and second cervicals are united. The five others are free and have long bodies, making the neck long. The caudal vertebrae form two distinct series, the first thirteen have large bodies, and are much higher than broad; the first nine have upper spinous apophyses well developed; and the first seven have transverse processes; the twelve chevron bones are very strong; the last nine caudal vertebrae are much depressed and they are twice as broad as high. Ribs 12: 12; the first four, only, have double articular surfaces; the first five are articulated to the sternum. The sternum is formed of three distinct bones, the front being the largest.

The pectoral fin is only rather longer than broad, and is not so long as the arm bones united: the blade bone is much extended in form and has the acromion and the coracoid well developed. The two bones of the fore arm are rather longer than the humerus. The radius is very broad. Carpal bones five, in two rows, the three upper ones being the largest: Metacarpals five. There is no phalanx for the thumb, only one for the little finger, six phalanges for the index finger, and four for the ring finger.

"The skull is rounded on all sides, the falx is ossified, the face is slender, the nasal canal open, the romer is shown above between the two intermaxillaries. The jaws have 32 : 29 teeth, of which two are in the intermaxillary bones. The teeth are conical, acute, rather far apart. The tympanid bone is two lobed. The petrous bones are without apophyses. The lower jaw is very high behind and curved, giving it the appearance of a Ziphius" (VanBeneden).

The animal under discussion possessed only fifty three vertebrae. The vertebral formula is: cervical 7, thoracic 12, lumbar 14, caudal 20–?21. The individual vertebrae agree very well with those of the type, except for abbreviations and elongations of the spinous and lateral processes. These variations are of no great importance as I shall later indicate. The union of the first and second cervicals and the long bodies of the others, are clearly shown (Fig. 37-*b*). The sternum is shown (Fig. 39-*a*).

The skull agrees fairly well with the original description. The rostrum is long, narrow and compressed (Fig. 40). The pterygoids are separate and divergent posteriorly (Fig. 41). The teeth do not agree in number with the type, the formula being 31 : 30. However, several of the teeth were immature and decidedly out of line. The others were so badly worn (Fig. 39-*b*) that only the slightest trace of enamel could be seen on a small number of them. It is virtually impossible to suggest the nature of the enamelled surface although in form, they were evidently slender and conical. The lower jaw is high behind and curved. (Fig. 42-*b*.)

Unfortunately the cartilaginous character of certain of the hand bones,

caused a loss of the thumb in the extraction and preparation of this organ. However, it will be noted that the humerus (Fig. 43) is shorter than the bones of the forearm and that the radius is broad. The carpals, metacarpals, and phalanges, are characteristic.

The tympanid bones (Fig. 44-*a*) are more definitely fixed and are, perhaps, of very important taxonomic value. The scapula is high and broad. The acromion and coracoid are well developed. (Fig. 44-*b*.)

In addition to the characters shown in the plates, the skeleton exhibited other features which might be of interest. The vertebra having the greatest dimension from tip to tip of the lateral processes, is the twenty-second which measures 12.7 cm. The vertebra having the greatest depth (craniad-caudad), is the atlas which measures 2.64 cm. The axis is the smallest in craniad-caudad depth, being only .59 cm.

The bodies of the thoracic and lumbar vertebrae, are almost circular. The centra of the first six vertebrae and those of vertebrae twenty-three to forty-three, inclusive, are also nearly circular. The seventh to the twenty-first vertebrae are somewhat flattened on the dorsal surfaces of the centra. There are concave indentations on the centra of the twenty-third to forty-third vertebrae. Number twenty-three shows the first sign of this indentation and there is a gradual increase in its depth until the fortieth. Beginning with forty-three and forty-four, the bodies of the vertebrae gradually become flattened dorso-ventrally, numbers forty-eight, forty-nine, and fifty, being the most noticeably so. Vertebrae numbers twenty-eight and twenty-nine, have concave indentations on their lateral spines. In a number of vertebrae, particularly, numbers fifteen, sixteen, seventeen, eighteen, and nineteen, the lateral processes are shorter on the left side. Vertebrae numbers twenty-one to fifty, seem to be almost bilaterally symmetrical.

While the specimen under discussion exhibits some differences from the type, there would be no justification for assuming that any or all of these differences are sufficiently distinct to be of specific or varietal value. Any attempt to separate a single individual with such marked similarities to a known species, could not be accepted in the light of conservative investigation.

In accounting for differences it must be borne in mind that the type was probably a female, while the present specimen is a male. Fischer (1881) states that the male rostrum is usually more elongated, more regularly tapering forwards, and less dilated in its middle portion, than that of the female. Usually the cranium is higher and the temporal fossae are more ovoid in the latter sex.

No dependence can be placed upon the number of teeth in discriminating species. This particularly applies to species in which there is a great number because those at the ends of the series are usually much smaller and frequently imbedded in the gums. In fact the number on one side may be greater than that on the other in the same animal.

Flower (1883) says "In all dolphins the form of the skull alters considerably with age. The rostrum or beak becomes larger in older animals, being both longer and wider in proportion to the brain case. The teeth become actually larger in consequence of a more considerable portion of the broad base of the crown arising out of the alveolus as the slender apex wears away, and they

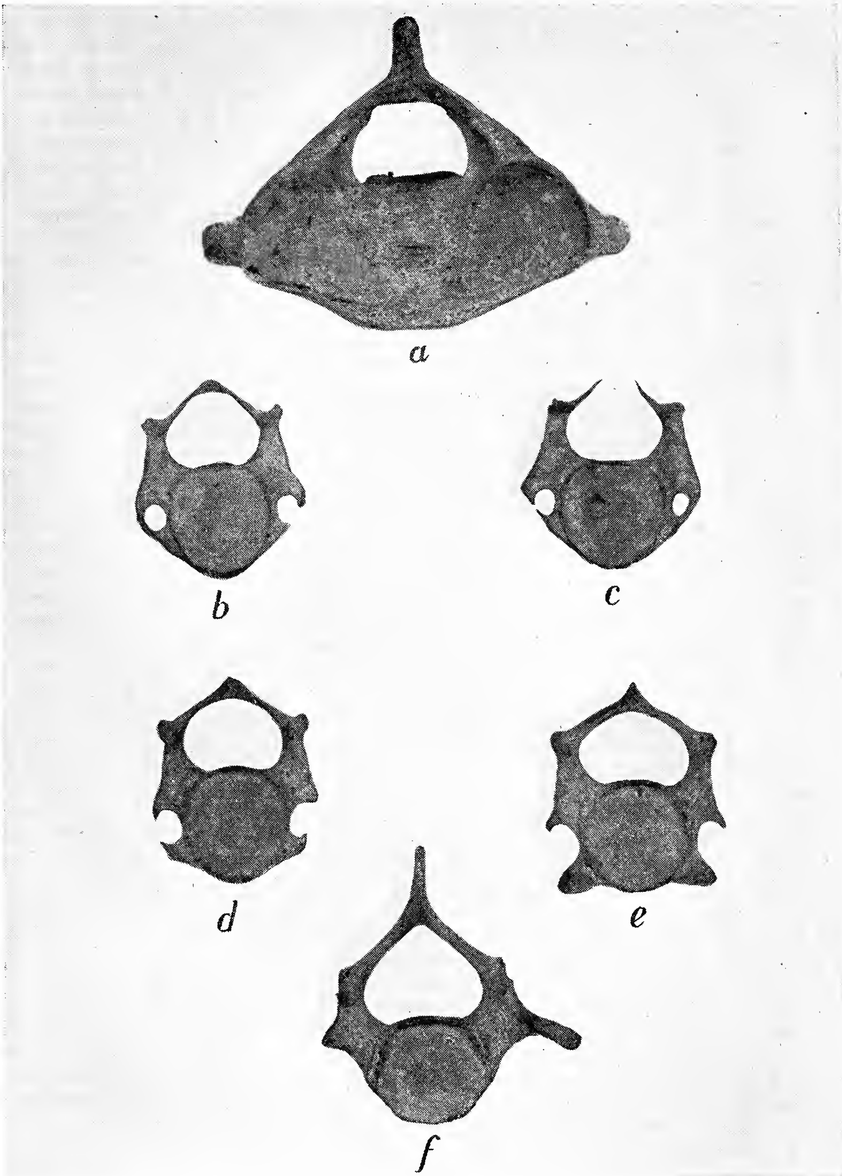


Fig. 45. *a, b, c, d, e, f, Sotalia guianensis* Van Beneden; *a*, axis vertebra; *b, c, d, e*, vertebra showing varying character of lateral foramina; *f*, vertebra with no indication of lateral foramina.

become more distant from each other through the growth of the maxillary bones. Thus the proportion of length and width of the beak, and the number of teeth in a given space, cannot be relied upon except in comparing adult animals. It is extremely difficult to tell the relative age of the individual as, contrary to what takes place in many other mammals, the sutures of the cranium close very early in the dolphins. Even the basilar suture which in seals, for instance, is united only with old age, no traces are left in dolphins about three-fourths grown, and in which the epiphyses are all free on the vertebrae and on the bones of the limbs, and of which the carpus is but imperfectly ossified."

The comparative osteology of the dolphin skeleton shows that it exhibits a series of wide variations, even within the individual, which contrast it noticeably with the greater constancy of the average mammal. The phylogeny of the Cetaceans would indicate that the osteoblastic structure of their skeletons would be far less compact than that of the domestic cat, for instance. Miller's treatise (1923) on the telescoping of the Cetacean skull indicates a lesser degree of fixity than is to be found in many other mammalian forms. Within the individual, there exists a wide variety of osteological peculiarities. The specimen under discussion exhibits many characters which fall within the range of individual differences. It might be well to direct attention to a few of these. The axis vertebra (Fig. 45-*a*) is shown. It is not completely ossified to form a neural canal. Another peculiarity is that the small lateral foramina on the right do not completely form a foramen, while the foramen on the left is complete. Fig. 45-*c* shows the complete enclosure of only one foramen. Fig. 45-*d, e* show vertebrae four and five to have only partial or semi-circular foramina. Fig. 45-*f* shows vertebra number six to exhibit no signs of lateral foramina. This part also shows only one prominent lateral process, the other being slight. The caudal vertebrae are far less fixed than the others, and certain phalangeal bones in the hand showed no degree of ossification.

In the determination of species on the basis of skeletal similarities, it is well to bear in mind the primitive character of certain modified parts. Much has been written on the subject of the modifiability of the Cetacean physiognomy. The increase in the number of phalanges and teeth, have been discussed at length by Kükenthal, Abel, Winge, and others. Even proportions, which in some rather definite mammalian forms, exhibit post natal changes, should be considered with extreme caution and viewed from an embryological basis. Only extremely obvious characters in the vertebral skeleton (of Delphinids), which in no way appear to be deformities, or, of pathological origin, should be considered in speciation.

Acknowledgements

The author wishes to thank Sir Sydney F. Harmer, former Director of the British Museum and Dr. M. Rauther, Director of the Würtemburg Naturaliensammlung in Stuttgart, for their assistance in establishing the exact locality and present location of the type, and for checking the results of his investigations.

To: Mr. Calvin Fisher Fencil, a Graduate Assistant in the Kartabo Party: Mr. Edgar P. Jones, Photographic Assistant: Mr. Theodore Fredley and Mr. Crane Remaley, graduate students in the Zoology Department, who generously assisted in preparing and photographing the specimen, the author is deeply grateful.

Dr. Gerrit S. Miller, Jr., of the United States National Museum, kindly supplied the photostatic copies of Van Beneden's plates, which are greatly appreciated.

Prof. Dr. Ferdinand Pax of the Zoologisches Institut and Museum in the University at Breslau, read and criticized the manuscript.

Especial thanks are due Professor Harold D. Fish and Dr. William Beebe for making these South American studies possible.

SAMUEL H. WILLIAMS

Zoologisches Institut and Museum der Universität Breslau,
November 29, 1927.

BIBLIOGRAPHY.

BATES, W. A.
1864 A Naturalist On The Amazon.

BEEBE, WILLIAM.
1925 Studies Of A Tropical Jungle, etc. Zoologica Vol. VI, No. 1.

CUVIER, G.
1829 Le Regne Animal d'apres son organization, pour servir de base a l'histoire naturelle des Animaux et d'introduction a l'Anatomie Comparee. Tome 5, 2nd Ed.

FISCHER, P. H.
1881 Cetaces du Sud-Ouest de la France. Actes de la Societe Linneene de Bordeaux.

FLOWER, W. H.
1870 Description of The Chinese White Dolphin (*Delphinus sinensis*). Transactions of the Zoological Society Of London VII, p. 159.
1883 On The Characters And Divisions Of The Family Delphinidae. Proceedings Of The Zoological Society Of London, pp. 476–513.
1888 Osteologie der Säugerthiere.

GERVAIS, F. P.
1855 Animaux nouveaux ou rares, recueillis pendant l'Expedition dans le partres centrales le l'Amerique du Sud. In Castelnau's Zoologie de l'Expedition dans le partres centrales de l'Amerique du Sud. Part VII.

GRAY, JOHN EDWARD.
1866 Catalogue Of The Seals And Whales In The British Museum, p. 257.
1868 Synopsis Of The Species of Whales And Dolphins in The Collections Of The British Museum.
1871 Supplement To The Catalogue Of The Seals and Whales In The Collections Of The British Museum, p. 401.
1856 Annals And Magazine Of Natural History series 2, XVII.

KUKENTHAL, WILLY.
1914 Untersuchungen an Walen. Jena Zeitschrift LI, pp. 90–91.

MILLER, GERRIT S., JR.
1918 A New River Dolphin From China. Smithsonian Miscellaneous Collections Vol. 68, No. 9.
1921 A translation of The Interrelationships Of The Cetacea by Adolph Winge. Smithsonian Miscellaneous Collections Vol. 72, No. 8.
1923 The Telescoping Of The Cetacean Skull. Smithsonian Miscellaneous Collections Vol. 76, No. 5.

OWEN, SIR RICHARD.
1866 On Some Indian Cetacea Collected by Walter Elliot Esq. Transactions Of The Zoological Society of London.

REYNOLDS, SIDNEY H.
1913 The Vertebrate Skeleton.

TRUE, FREDERICK W.
1889 A Review Of The Family Delphinidae. Bulletin U. S. National Museum No. 36.

VANBENEDEN, P. J.
1864 Sur un Dauphin Noveau (*Delphinus guianensis*), et un Ziphioide rare. Manifestation En L'Honneur P. J. VanBeneden, p. 27. Opusc. Coll. 1857–1887. Louvain.
1863 Memoires Corrones de l'Academie de Royale de Belgique. Collection in octavo, Tome XVI, Mem. 2, p. 23.
1875 Memoires de l'Academie de Belgique XLI.

VAN BENEDEN ET GERVAIS
1880 Osteographie des Cetaces, Vivants et Fossiles.

New York Zoological Society

OBJECTS OF THE SOCIETY

A Public Zoological Park. A Public Aquarium. The Preservation of our Native Animals. The Promotion of Zoology.

ZOOLOGICA VOL. I

		Paper	Cloth
Parts 1–20	*Not bound*	3.85	
Parts 1–20	*Bound*		6.00

Postage-weight, 4 pounds

Zoologica Vols. I, II and III completed and indexed.
Subjects in Vols. I and II furnished on application.

ZOOLOGICA VOL. II

		Paper	Cloth
Parts 1–18	*Not bound*	4.30	
Parts 1–18	*Bound*		6.50

Postage, weight, 4 pounds

ZOOLOGICA VOL. III

	Paper	Cloth
1–2—Objects, Tropical Research Station (*Osborn*)	.25	
Contributions Tropical Research Station (*Beebe*)		
3–11—Social Beetles, British Guiana (*Wheeler*)		
Tachigalia Ants (*Wheeler*)		
Habits of Cucujidae (*Wheeler*)		
New Coleoptera (*Schwarz-Barber*)		
Larvae, Pupae, Social Beetles (*Boving*)		
New Diadiplosis (*Felt*)		
New Blepyrus (*Brues*)		
Tachigalia Membracids (*Herbert Osborn*)		
New Entomobrya (*Folson*)	1.00	
12—Fetuses, Guiana Howling Monkey (*Schultz*)	.50	
13—Mammals Collected Tropical Research Sta. (*Anthony*)	.25	
14–15—New Batrachians (*Noble*). New Lizards (*Noble*)	.25	
16—Descriptiones Termitum in Anglorum Guiana Reportorum (*Silvestri*)		
17—New Genera and Species, Termitophilous Coleoptera (*Mann*)		
18—Glandular Structure, Abdominal Appendages, Termite Guest (*McIndoo*)		
19—Termitophilous Apterygota (*Folsom*)		
20—Three Apparently New Species, Termitaphis (*Morrison*)		
21—Termitophilous Millipeds (*Chamberlin*)	.75	
22–23—A Termitophilous Braconid (*Brues*). Two Myrmecophilous Phoridae (*Brues*)	.25	

ZOOLOGICA VOL. IV

	Paper
1—Fishes, Amphibians, Reptiles (*Breder*)	.15
2—Frozen Mammoths (*Lang*)	.25
3—Galapagos Tortoises (*Townsend*)	.50
4—Some Panama Fishes (*Breder*)	.20
5—Locomotion of Fishes (*Breder*)	1.25

ZOOLOGICA VOL. V

	Paper	Cloth
1—Williams Galapagos Expedition (*Beebe*)	.15	
2—Galapagos Heterocera (*Schaus*)	.20	
3—Galapagos Lepidoptera (*Beebe*)	.15	
4-16—Ichthyology (*Nichols*)		
Apterygota (*Folsom*)		
Homoptera (*Osborn*)		
Mallophaga (*Ewing*)		
Diptera (*Johnston*)		
Arachnida (*Banks*)		
Formicidae (*Wheeler*)		
Triungulin Larvae (*Brues*)		
Chilopods (*Chamberlin*)		
Coccidae (*Morrison*)		
Brachyuran Crabs (*Rathbun*)		
Macrura and Anomura (*Schmitt*)		
Hymenoptera (*Rohwer*)	.50	
17—Neuroptera (*Banks*)	.15	
18—Isopods (*Van Name*)	.25	
19—Copepods (*Wilson*)	.15	
20—Coleoptera (*Mutchler*)	.20	
21—Hemiptera-Heteroptera (*Barber*)	.15	

ZOOLOGICA VOL. VI

	Paper	Cloth
1—Ecology of Kartabo (*Beebe*)	1.00	
2—Birds of Kartabo (*Beebe*)	.35	
3—Membracidae of Kartabo (*Haviland*)	.30	
4—Termites of Kartabo (*Emerson*)	1.00	
5—Ispods of Kartabo (*Van Name*)	.30	

ZOOLOGICA VOL. VII

	Paper	Cloth
1—Three-Toed Sloth (*Beebe*)	.60	
2—Development of Soldier Termites (*Emerson*)	.25	
3—A New Polychaetous Annelid (*Treadwell*)	.10	
4—A River Dolphin from Kartabo (*Williams*)		

ZOOLOGICA VOL. VIII

	Paper	Cloth
1—The Arcturus Expedition (*Beebe*)	.50	
2—Arcturus: Equipment and Operation (*Tee-Van*)	.60	
3—Brotulid Fishes (*Trotter*)	.20	
4—Galapagos Brachyura (*Boone*)	1.40	
5—Embryology of American Eel (*Fish*)	.30	
6—Studies on Body-Forms of Fishes (*Gregory*)	.75	
7—Annotated List of Synentogathi (*Nichols-Breder*)	.45	
8—Polychaetous Annelids (*Treadwell*)		
9—Sea Stars from the Arcturus Expedition (*Fisher*)		
10—Scyphomedusae (*Bigelow*)		

ZOOLOGICA VOL. IX

	Paper	Cloth
1—Marine Fishes—New York and So. New England (*Nichols-Breder*)	1.40	
2—Inquilinism (*Gudger*)	.15	
3—Frog Tagging (*Breder-Redmond*)	.30	
4—Turtle Trailing (*Ruth Breder*)	.25	
5—Functions and Morphology (*Parr*)	.25	
6—Uruguayan Fur-Seal Islands (*Smith*)	.25	

Publications of the Society for sale at the Zoological Park, 185th Street and Southern Boulevard, New York City.

ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE
NEW YORK ZOOLOGICAL SOCIETY

VOLUME VII. NUMBER 5

THE REDUVIIDAE OF KARTABO
BARTICA DISTRICT, BRITISH GUIANA

By Maud D. Haviland (Mrs. H. H. Brindley).
Sometime Fellow of Newnham College, Cambridge.

PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

December, 1931

New York Zoological Society

General Office: 101 Park Avenue, New York City

THE REDUVIIDAE OF KARTABO

BARTICA DISTRICT, BRITISH GUIANA.*

By Maud D. Haviland (Mrs. H. H. Brindley).

Sometime Fellow of Newnham College, Cambridge.

(Figs. 46–47.)

Introduction.

The first of this series of communications on the Rhynchota of Kartabo dealt with the Membracidae of the area and was published in 1925. (*Zoologica, vol. vi, no. 3.*) The following study of the Reduviidae is based partly on my own collection made between June and September, 1922; and partly on the collection formed by other workers at the Station in previous years, and which has been kindly placed at my disposal by Mr. Beebe. In addition I have included certain species that I collected in October along the Demerara and Berbice Rivers, and which have not yet been recorded from Kartabo, although it is probable that they occur there also. Where no locality is given in the following pages, it is to be understood that the species in question was collected at Kartabo Point.

The types of the new species described here are in the British Museum of Natural History. As in my previous paper, the synonymy makes no pretension to completeness but indicates merely where a reliable earlier description can be found. The following abbreviations have been used:

H.F. = Hemiptera Fabriciana } Stal, *K. Sven. Vet-Akad. Handl.*
E.H. = Enumeratio Hemiptorum } Stal, *K. Sven. Vet-Akad. Handl.*
B.C.A. = *Biologia Centrali-Americana.*

General Observations.

Thanks to the labours of the compilers of the *Biologia Centrali Americana*, the hemipterous fauna of Central America has been recorded, and the results of the collections examined and published, in greater detail than has been possible for much of the even larger forested region of northern South America which lies east and south of the valley of the Orinoco, and includes the greater part of the

* Contribution, New York Zoological Society, Department of Tropical Research, No. 364.

basin of the Amazons. Hence attempts to compare the Reduviid fauna of Central America and Brazil are probably misleading; and any inferences drawn therefrom will require modification as new knowledge is obtained as to the range of many species, and the determination between geographical races and colour varieties becomes more exact. How much more remains to be discovered from the point of view of distribution alone may be judged from the fact that even the small area of Kartabo Point has added to the Guiana list ten species already described but not previously recorded from the country. If deductions from the small collection under review are permissible, it may be suggested that three elements go to make up the Reduviid fauna of Guiana. There is a northern element of species belonging to groups whose headquarters are in Central America, and a southern or Brazilian element of forms known chiefly from the Amazon region. The third and largest element consists of species which are widely distributed over the tropics of the New World. There are numerous genera, and species also, which range from Mexico to Southern Brazil and even to the Argentine. Some of these are variable insects, but in most cases the varieties can as yet hardly be assigned to different geographical boundaries.

Genera such as *Saica, Gnathobleda,* and *Sinea* appear to have their headquarters in Central America. Others such as *Mestor, Mindarus, Calliclopius, Zirta,* etc. suggest a Brazilian element in the Guiana fauna. On the whole, ignoring the wide ranging forms, the southern element seems to prevail over the northern in the area under review. Thus of the forty-one species (belonging to thirty-one genera) in the collection which have been previously described, sixteen species (thirteen genera) are widely distributed in the tropics from Brazil to Mexico. Seven species (seven genera) have been hitherto recorded from Central America and Guiana only, but five of these belong to widely distributed genera. Twelve species (seven genera) suggest the Brazilian element, and five of these genera are not included in the B. C. A. To these should doubtless be added six species (six genera) which have hitherto been recorded from Guiana only, and three of these genera are not so far known in Central America.

To sum up—twenty-three of the thirty-one genera recorded from Kartabo are included in the B. C. A.; but this does not indicate

so much a preponderance of Central American forms in the area, as the great range of many neo-tropical Reduviidae. In fact the evidence, such as it is, is much what we might expect from a study of the map of South America. The Amazons valley, with the Guiana coast lands and the valley of the Orinoco, form a continuous homogeneous zoogeographical region, closed at its northwest angle by the Cordilleras of Venezuela and Colombia. This line of open hilly country has acted as a natural oecological barrier to the range of certain species, determining that this family at all events shall be divisible into a Central American and a Brazilian group, and that the latter shall predominate in the fauna of Guiana.

From the point of view of its Reduviidae, the collecting ground at Kartabo Point consists of two formations only—the shade jungle, and the clearings and forest trails. Of the two, the second is incomparably the richer both in species and individuals. Those found in the dark jungle are for the most part obscure bark-living forms such as *Ghilianella,* or *Leogorrus;* while the shrubs bordering the clearings and trails are populated with *Zelus, Notocyrtus,* and *Xystonyttus,* and the open ground and herbage provide *Ricolla, Spiniger, Phymata,* etc. In fact the Reduviidae of Kartabo could be divided oecologically into bark-loving and foliage loving groups. The distinction is more one of mode of life than of affinities. Thus *Apiomerus hirtipes,* though it sometimes appears in light places, prefers dark termite-infested timber in the forest gloom; but *Calliclopius nigripes* according to my experience, is a light loving species and taken only on low foliage round the clearings. Food is probably the most important factor in the local distribution of these predatory bugs, but our knowledge of the subject is less than could be wished. Reduviidae, though often swift upon the wing, are usually sluggish hunters and it is not easy to determine their natural prey. In captivity I found that their tastes were more catholic than I had supposed, but experiments on the appetites of captive animals are not always reliable.

The three great classes of food for insects in the tropical forest as elsewhere are of course the living tissues of animals, the living tissues of plants, and the detritus formed by the decomposition of both. To seize and crush the tissues, especial organs are necessary, and only certain insects possess the requisite apparatus. Such are most adult Coleoptera and Orthoptera, some specialized adult forms of other families, and the larval and nymphal stages of most families

except the Rhynchota. Bugs at every stage, and the adults of all Lepidoptera, most Diptera and some Hymenoptera etc., like the stork in the fable, can only imbibe liquid nourishment. For these the tropical forest contains two easily tapped sources of supply of animal and plant juices respectively. For carnivorous forms, there are termites. Ubiquitous, abundant, and relatively defenseless, their plump bodies are the staff of life to many animals besides insects, and they are among the most persecuted creatures in the jungle. Phytophagous forms can readily obtain plant sap in the shape of the "honey-dew" excreted by Homoptera, which, though not a complete diet in itself, offers a concentrated and readily assimilated food. Honey-dew as an oecological factor in the tropical forest has received less attention than it deserves. Together with the extra-floral nectaries which are characteristic of so many jungle plants, it partly takes the place of the nectar of flowers which are comparatively absent in the forest below the level of the tree tops. Fancifully the vegetation of the rain-forest may be regarded as a country with an abundant underground water supply and inhabited by a huge thirsty population which flourishes only by assiduous attention to millions of little suction pumps. The water supply is the plants' sap; the pumps are the hosts of Membracids, Jassids, Coccids, etc. who ceaselessly suck up the sap and then convert and extrude it in shining sticky flecks upon the leaves; the population are the innumerable flies, bees, ants, moths and butterflies, etc. which feed greedily on this saccharine food.

Several of the Kartabo Reduviidae feed mainly if not exclusively on termites. Such are *Leogorrus litura, Apiomerus hirtipes, Sorglana pallens;* and some of the Ploiariinae such as *Ghilianella brevicornis* will eat them, at any rate in captivity. But our list contains a number of species which haunt open foliage in clearings and trails through the secondary growth rather than deep shade forest and standing timber. The prey of these insects is difficult to determine. *Debilia fraudulenta* for instance has been known to suck Jassid nymphs; and I have obtained individuals of *Zelus pallidinervis* and *Zelus erythrocephalus* feeding on small flies and a medium-sized spider respectively. Some of these foliage loving species, such as *Zelus, Repipta, Ricolla* etc. certainly supplement an insect diet with honey-dew from Homoptera, and with the secretion from the extra-floral nectaries of plants. *Notocyrtus gibbus* in particular can

be captured with certainty on any of the jungle plants which are well provided with these organs. In no case have I observed saprophytic feeding among the Kartabo Reduviids; and this is somewhat remarkable considering the amount of decaying organic matter present in the forest, and that some of the Coreidae of the locality (for instance *Hyalymenus pulcher*) seem to live largely, not on sap, but on the liquid from the decomposition of vegetable matter in the axils of the leaves of forest plants. Several of the Kartabo Reduviids are commonly taken at light. Such are *Mindarus basalis*, the three species of *Rasahus*, *Rhodnius prolixus*, *Sirthenia stria* and *Eratyrus mucronatus*. *Gnathobleda maculosa* has also been taken in this way.

The neotropical Reduviidae offer such remarkable instances of Müllerian mimicry that it is rather strange that they have not been more studied from this point of view. In this respect they offer a contrast to the two dominant vegetable-feeding families of bugs of the same region. The Coreidae and Pentatomidae possess as a rule either procryptic[1] or aposematic (simple warning) colouration, and examples of mimicry are not common among them. Some predatory bugs have a procryptic appearance—*Dysodius lunatus* and *Sorglana pallens* are almost indistinguishable from the flakes of bark over which they glide; *Phymata erosa* is invisible among the green panicles of the grass to which it clings. Many others are gaudy and conspicuous in colouring, such as *Acanthiscium superbus*, *Mindarus basalis*, and *Calliclopius nigripes*. But a number of species whose form and colour can be classified are Müllerian mimics, and at Kartabo they form their most striking associations with Hymenoptera.

The three outstanding groups of the area are: the Pompilid group, the Ichneumonid group, and the Meliponine group. The models of the first association are the great jungle Pompilidae. Some of the genera *Chrysobapta*, *Priocnema*, etc. possess tawny wings and antennae and black metallic bodies. In both form and colour, *Spiniger spinidorsis* bears a remarkable resemblance to these hunting wasps, which was noticed first by Bates and later by Belt and others. Besides the Pompilid and *Spiniger spinidorsis*, this association at Kartabo includes the yellow and black Locustid *Scaphura nigra*, a

---

[1] The convenient terms proposed by Poulton to define different kinds of form and colour are used here.

large black fly (sp?) with yellow antennae, and a Mantispid. (Beebe, *Zoologica, vol. vi, no. 1.*) The wasps are very common in the area, but the rest of the participants are comparatively rare. *S. spinidorsis* comes next in point of numbers, but it is decidedly scarce. The wasp models are probably the least molested insects in the jungle, and their powerful flight and strong sting are well advertised by their conspicuous colouring. The bug exudes a strong odour when handled, and its sharp thoracic spines are perhaps an additional defense. It is not known what protection the other members of the association have, but we are probably justified in regarding them as Müllerian rather than as Batesian mimics. Two other species of the genus *Spiniger* found at Kartabo belong to Müllerian associations also centering around hunting wasps. *S. nigripennis* in appearance and haunts resembles some of the large black Pompilidae which are common in the clearings and forest trails. The Syntomid moth *Pompiliopsis tarsalis* is another member of this association, and resembles its hymenopteron model both in appearance and behaviour. *Spiniger mustelinus* again is linked to a third form of hunting wasp typified by *Sphex ichneumoneus* which is yellow in colour. There are no more striking examples of convergent colour pattern for mutual protection than that of these three bugs of the same genus, almost identical in structure and habits but differing in conformity with the three colour types of wasps of different families which inhabit the same area. As Poulton has pointed out, Müllerian mimicry is not mimicry in the strict sense of the word but is really the possession in common of warning colouration by unrelated forms. The larger the number of participants in a Müllerian association, the wider is the advertisement of that particular type and the greater the advantage to the members. The genus *Spiniger* is of great interest in this respect, and is almost divisible into two groups: hymenopteron mimics and forms which possess only simple warning (aposematic) colouration. With sufficient material it seems even possible to trace the line of evolution from one to the other. The members of the former group agree in their black and yellow colouring, but within these limits every variation exists, and probably several species are no more than varieties of the one or other of the three major types. The livery has been patented as the corollary of a sting or of a noxious taste and exact adherence to details does not greatly matter; for the

enemy who has once fallen victim to either will take no risks a second time. The modelling of the female abdomen of these bug wasp-mimics is specially remarkable. The constricted "waist" is passably simulated, and the curved and pointed terminal segments are a wonderful reproduction of the hymenopterous sting. Comparison of the female genitalia of *Spiniger* with that of some other Acanthaspidinae such as *Leogorrus* would suggest a striking modification of external structure to appearance were it not that our ignorance of the life-history of these bugs makes it possible that perhaps the form of the abdomen is not really the imitation of the wasp's sting but is actually a comparable organ, in use as an ovipositor.

A second hymenopteron-heteropteron Müllerian association which is widely spread in tropical America is that focussed round some of the big Ichneumonoidea with yellow-hyaline banded wings and red bodies. The bug participants at Kartabo belong to the genera *Xystonyttus,* and *Graptocleptes* among the Reduviidae, and to some of the *Monalonion* group among the Miridae.

The third association between these two great orders is that of certain Meliponine bees and the genus *Notocyrtus.* The broad flat head and thorax of the bee are reproduced by the angular inflated pronotum of the bug, whose own head is almost concealed in life; and the hyaline hemielytra and dilated hind-tibiae of *Notocyrtus* bear out the resemblance to the bee with its "pollen-baskets" on the legs. The bugs live on open foliage, and may often be taken sipping nectar, or honey-dew from Homoptera colonies. The movements of the bug are quite bee-like, and I have several times been deceived by the mimicry. The Meliponinae visit the same places in search of nectar or resin, and it is not uncommon to see model and mimic side by side. At Kartabo the dominant Meliponinae are black, and the yellow forms seem to be rather scarce, but both yellow (*N. dorsalis*) and black (*N. gibbus*) bugs are found. Meliponine bees are stingless, and at first I was at a loss to account for the advantage to the hymenoptera in this association, especially as they are so much more abundant than the bugs. However Wheeler (*Psyche, no. 20, 1913*) has recorded that a Central American species can emit a fluid caustic enough to burn the human epidermis, and it is quite likely that others also possess this power, which would render them unpalatable to birds, etc.

List of Species.

Series ANONYCHIA.

Superfamily Reduvioidea.

Phalanx Reduviiformes.

Family I. Macrocephalidae.

Subfamily Phymatinae.

Family II. Reduviidae.

Subfamily I. Ploiariinae.

Subfamily II. Saicinae.

Subfamily III. Stenopodinae.

Subfamily IV. Acanthaspidinae.

Subfamily V. Piratinae.

Subfamily VI. ECTRICHODIINAE.

Subfamily VII. APIOMERINAE.

Subfamily VIII. HARPACTORINAE.

Subfamily PHYMATINAE.

Phymata erosa (Linn.) var. *fasciata* (Gray).

Phymata erosa, var. *fasciata*, Champion, *B. C. A., Heteroptera, II, 1901.*

According to Champion, this is a North and Central American form and has not yet been recorded from Guiana. The examples in this collection, though rather smaller than those he figures, appear to belong to this variety. This species was not common at Kartabo in the summer, but was more frequent near the coast. It occurred abundantly in a cocoanut palm swamp beside the

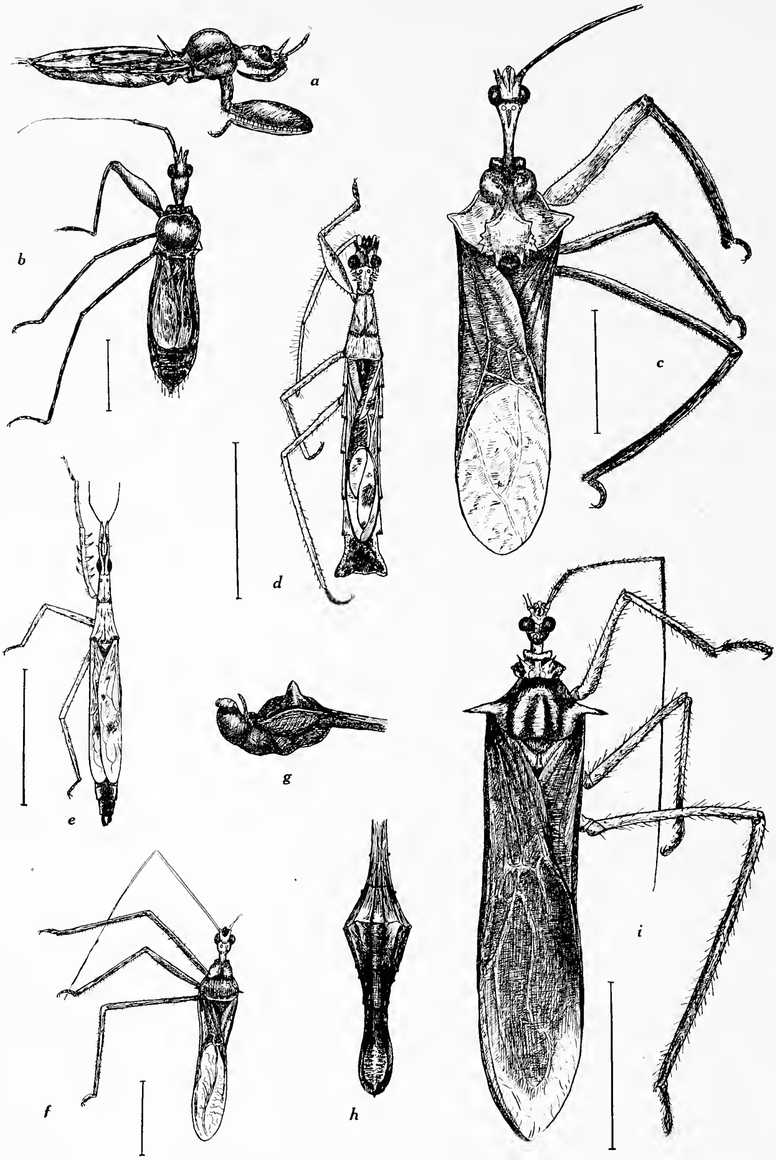


Fig. 46. *a*, *b*, *Vescia adamanta*; *c*, *Acanthiscium superbus*; *d*. *Gnathobleda maculosa*; *e*, *Pnirontis demerarae*; *f*, *Repipta affinis*; *g*, *Ghilianella brevicornis*, apex of abdomen of male; *h*, *Ghilianella andersoni*, apex of abdomen of male; *i*, *Spiniger mustelinus*, female.

Demerara River at Diamond Plantation. With their raptorial forelegs, the insects cling to the panicles of flowering grasses, amid which their variegated green colouring is almost invisible.

Gardena faustina McAtee.

Gardena faustina, McAtee, *Proc. U. S. Nat. Mus., vol. 67, 1926.*

One male taken, 12. 10. 22. In this example in life the mesothorax was black and the rest of the body was pale chestnut.

Ghilianella andersoni, sp. nov.

(Fig. 46, h).

A single example taken on a tree trunk in dark swamp jungle in September is provisionally described here as new. It is evidently close to *G. pascoei* Bergroth, but differs in certain particulars. The head and thorax are finely granulated and covered with patches of short castaneous hair. The seventh abdominal tergite is rounded, and terminates apically with a short, abrupt, and almost spine-like process which scarcely reaches the border of the hypopygium. The abdomen is widest across the fourth tergite. The posterior margins of abdominal sternites 2–5 are slightly, and the sixth is more markedly, sinuate. The spiracle of the seventh segment is pedunculate and not included within the border of the segment.

I have pleasure in naming this species after Mr. J. Anderson of Plantation Diamond, in recognition of his kind assistance during my residence in the colony.

Ghilianella brevicornis, sp. nov.

(Fig. 46, g).

This form may be only a variety of *G. mirabilis* McAtee, described from the Amazons region. It differs in that the horns of the abdominal expansion of the male are shorter and more flattened in the dorso-ventral plane and more carinate on the outer margin. The width between the diverging tips of the horns is only 2.5 mm., as against 5.0 mm. in *G. mirabilis.*

Ghilianella glabrata McAtee.

Ghilianella glabrata, McAtee, *Proc. U. S. Nat. Mus., vol. 67, 1926.*

A female taken 1. 8. 22, on a tree trunk in dark shade forest on the Cayuni River.

Saica recurvata (Fabr.).

Saica recurvata, Stal, *H. F., I, 1868.*

This species is not uncommon at Kartabo from July to September. It frequents sunny clearings with low thick vegetation upon which it rests in conspicuous places and takes wing only with reluctance. The examples from this locality are somewhat pale in colour, and yet are too dark to be assigned to the allied species, *S. ochracea,* Distant.

Gnathobleda maculosa, sp. nov.

(Fig. 46, d).

Elongate, narrow, pale greyish ochreus; head, pronotum and scutellum pitchy-brown; rostrum spotted with brown; a narrow dark line extending along the sides of the thorax above the coxae from the prosternal spines; a dark median line extending from the anterior margin of the mesosternum to the apex of the abdomen; the dorsal surface of the abdomen, especially at the posterior end, spotted with dark brown. Elytra with pallid venation, but with the corium, clavus, and membrane boldly spotted with brown, and with a broad brown patch at the inner distal angle of the corium. Antennae pale, with the first and second joints infuscate. Legs pale ochreus, sparsely spotted with pale brown and a conspicuous dark spot at the tibio-tarsal articulation.

Head sub-oblong, the ante-ocular portion a little longer than the post-ocular, deeply transversely sulcate behind the eyes; eyes very prominent; antenniferous tubercles furnished with small spines and a pair of sharp diverging frontal tubercles between them; post-ocular margin with four or five small simple spines; rostrum with the first joint equal in length to the second and third together; antennae thickly hairy, the first and second joints equal in length.

Prothorax oblong, narrow and sub-tuberculate at the anterior angles, spinous along the lateral margin, somewhat rugose behind; prosternum with two sharp forward-projecting spines in front and the pleura with spinous dilatations above the coxae.

Scutellum triangular, acuminate, longer than wide, furnished with a blunt porrect conical tooth which has a minute tubercle immediately behind it.

Abdomen very elongate, narrow, oblong, slightly notched at the lateral expansions, and with the terminal segments somewhat dilated and flattened laterally.

Anterior coxae inserted far forward; trochanters unarmed; anterior femora incrassate, roughly spinose, and hirsute; tibiae without spongy fossae; tarsi with the apical joint much the longest, the basal joints doubtfully distinct.

Elytra reaching to the apex of the penultimate abdominal segment.

Long. 19 mm. Lat. 4 mm.

Type: Male.

Two males recorded from Kartabo—one undated, the other caught at the laboratory light in June, 1922.

Pnirontis demerarae, sp. nov.

(Fig. 46, e).

Elongate, narrow, sub-fusiform; pale testaceus yellow, darker on the sides of the thorax and dorsum of the abdomen, femoral and tibial spines annulated with brown.

Head elongated, as long as the pronotum, the post-ocular portion rather shorter than the ante-ocular portion, with a median sulcus; eyes not prominent; ocelli, small, red; genae very prominent; basal joint of the antenna short, blunt, extending less than one third beyond the articulation of the second

joint; the latter when extended backward attaining the anterior margin of the eye; post-ocular spines six in number, the fifth bifurcated. Pronotum granulate, rugose, longer than broad, narrow in front, carinate laterally, with a pair of stout sharp spines projecting forward from the anterior angles, and with a shallow median sulcus; hind margin somewhat swollen and depressed.

Scutellum small, and with a small tooth at the apex.

Abdomen tapering back from the fourth segment, the first five segments carinate below; the first genital segment concave at the apex, the second forceps-shaped. Legs short and pilose; anterior femora furnished on the outer edge with five, and on the inner edge with four long spines; tibiae armed on the inner side with three stout spines of which the first is much the longest; and on the inferior surface, close to the tarsal joint, is a compressed pilose tubercle. Elytra reaching the base of the fifth abdominal segment; wings white, semihyaline.

Long. 19 mm. Lat. 2.5 mm.

Type: Female.

A single example was taken by sweeping at Diamond Plantation (Demerara) in October. This species differs from *P. spinimanus* Champion in the colour, greater size, number and arrangement of the spines of the legs, etc.

Pnirontis infirma Stal.

Pnirontis infirma, Stal, *O. V. A. F., 1859.*

A female example taken at Kartabo in June seems to be a dark slender form of this species.

Stenopoda culiciformis (Fabr.).

Stenopoda culiciformis, Stal, *H. F., 1868.*

This species is not uncommon at Kartabo and occurs chiefly on the tops of grasses and on low shrubs in sunny clearings. When handled, it smells pleasantly of pineapple. The orange dorsum is concealed in the resting attitude, and the insect then bears a curious accidental resemblance to some of the straw-coloured short-horned grasshoppers which are common in the same places. The likeness is enhanced by the angular flexure of the long hind legs, and by the antennae, which are bent down sharply so as to expose to view only the thickened basal portion.

Eratyrus mucronatus Stal.

Eratyrus mucronatus, Stal, *Berl. Ent. Zeit., III, 1859.*

This species is occasionally taken at light at the Station.

Leogorrus litura (Fabr.).

Leogorrus litura, Stal, *H. F., I, 1868.*

L. litura lives on and under the bark of standing timber, and sometimes occurs in some numbers on the same tree. The nymphs, like others of this group, may be found in termite nests; and as they exude a viscous fluid, their bodies become covered with dust and fragments of wood until they resemble nothing so much as small animated rubbish heaps.

Mestor geniculatus (Burm.).

Mestor geniculatus, Stal, *Berl, Ent. Zeit., III, 1859.*
Mestor n. n. Lamus, Kirkaldy, *Ent., 1904.*

Two examples dated 10. 10. 20, and 12. 6. 22 respectively. Both are somewhat dark in colour.

Vescia adamanta, sp. nov.

(Fig. 46, a–b).

Moderately stout, brachypterous, non-ocellated; rusty black; antennae, legs, and spine of scutellum ferruginous; a spot on the outer margin of the membrane, the claval suture, and some large spots on the dorsum and sides of the abdomen pale ochreus; head, pronotum, and fore femora polished and shining; underparts of body and the legs densely clothed with short light hairs, the anal region and the under surface of the fore femora with stiffer and longer hairs. Head oval, the post-ocular a little longer than the ante-ocular portion, swollen behind the eyes and then constricted at the neck, furnished with a straight forward projecting spine between the eyes; eyes not more prominent than the lateral post-ocular margins of the head; antennae shorter than the body, with the first and second joints thickened, the first claviform, the second fusiform and rather more than half as long again as the first, the terminal filiform joints thickly beset with hairs.

Pronotum with the anterior lobe inflated, rounded, declivous behind, with a faint median sulcus, and with a carinated depression extending on either side of the disc horizontally; furnished on the anterior aspect of the prosternum with two minute setiferous tubercles; posterior lobe short, sub-pentagonal, and armed with four short stout dorso-ventrally flattened divergent tubercles or teeth. Scutellum triangular, rugose, and furnished with a long straight backward projecting spine. Metasternum and first five sternites of the abdomen carinate. Elytra extending almost to the base of the sixth abdominal tergite; venation obscure.

Legs moderately long and rather stout; fore femora greatly incrassate, slightly incurved, narrowing towards the apex, flattened beneath, and furnished with two rows of minute setiferous tubercles.

Long. 9 mm. Lat. 2.5 mm.

Type: Female.

A single example taken in October at Plantation Diamond from the debris collected under the fibre round the bole of a cocoanut palm beside the Demerara River. I am indebted to the late Dr. Bergroth for the generic determination of this species.

Rhodnius prolixus Stal.

Rhodnius prolixus, Stal, *Berl. Ent. Zeit, III, 1859.*

Not uncommon at Kartabo and sometimes taken at light.

Sorglana pallens (Laporte).

Macrophthalmus pallens, Stal, *E. H., II, 1871.*
Sorglana n. n. Macrophthalmus, Kirkaldy, *Ent., XXXIII, 1900.*

I took a single example of this species on a tree trunk, 18. 8. 22. It does not seem to be very common at the Station.

Spiniger mustelinus, sp. nov.

(Fig. 46, i).

Elongate, robust, body matt, smooth, the legs and antennae moderately hairy; head ochre yellow, with a fuscous patch at the base of the genae and gula, and a broad dark transverse band between the eyes extending back to include the ocelli; rostrum and antennae dark yellowish brown; pronotum ochre-yellow shading to orange, disc of the anterior lobe outlined with brown and with a brown U-shaped band over either shoulder; transverse sulcus brown; posterior lobe with two broad incomplete median brown bands, outside which on either side are a pair of narrower bands extending backwards from the transverse sulcus to the posterior border, and joined on each side by a broad dark band extending upwards obliquely across the base of the lateral spines; scutellum brown with a yellow border and spine; under parts dirty yellow. Abdomen pitchy brown, the first three segments spotted with pallid yellow. Elytra yellow, clouded with brown and with a dark mark on the interior margin of the membrane. Legs yellow with brown tarsi, the posterior femora and tibiae broadly marked with brown. Antennae slightly pubescent; legs and the apex of the abdomen clothed with long sparse hairs.

Head oblong, the jugae not raised, the genae obtuse at the apex; eyes large, occupying the whole side of the head; ocelli prominent and slightly elevated; antennae moderately long, first joint stout, sub-claviform, less than half the length of the second, the succeeding joints very slender and filimentous. Pronotum smooth, the anterior lobe sub-quadrate, wider than long; furnished with two long yellow outwardly diverging spines on the disc and two small conical lateral tubercles; posterior lobe wider than long, with the posterior border slightly sinuate and depressed, and the lateral margins strongly dilated and produced into two long spines. Scutellum furnished with a long semi-erect spine. Abdomen narrow at base and widening to the fourth segment; abdominal sternites 1–3 carinate; apex sharply reflexed. Elytra extending beyond the tip of the abdomen. Legs elongate, the anterior femora armed beneath with five or six minute blunt tubercles; the anterior tibiae with a few very small tubercles and a spongy fossa extending up about one-fourth of the shaft.

Long. 24 mm. Lat. 8 mm.

Type: Female.

This handsome insect belongs to the sub-genus *Acrocoris*, according to Stal's division of this large genus. I obtained two females in July and September respectively. In both cases they were running over rough sandy soil in a forest clearing. Like *S. spinidorsis* this species is an excellent mimic of certain large yellow fossorial hymenoptera which frequent the same bare gravelly places.

Spiniger nigripennis Stal.

Spiniger nigripennis, Stal, *E. H., II, 1871.*

This species is evidently rare at Kartabo. Superficially it resembles *S.*

ater, St. F. and S.; but the genae are acute, and the thoracic spines are long as in *S. spinidorsis*. It is evidently a mimic of the black Pompilidae of the region, and moves in a wasp-like manner over the foliage of the forest trails which appear to be its haunts.

Spiniger rubropictus (H-Sch.).

Spiniger rubropictus, Stal, *Berl. Ent. Zeit., 1869.*

This species has been recorded a few times from Kartabo.

Spiniger spinidorsis (Gray).

Spiniger spinidorsis, Stal, *E. H., 1871.*

This magnificent insect occurs at Kartabo though apparently it is not very common there. It emits a strong though not disagreeable odour when handled. I have commented elsewhere on the resemblance of these bugs to hymenoptera. It is less striking when the insects are at rest owing to the different carriage of the wings.

S. obscuripennis, Stal is probably a variety of this species. Otherwise the Kartabo examples, which have pale spines, might be assigned to that form, although the wings are unspotted.

Melanolestes morio (Erichs.).

Melanolestes morio Stal, *O. V. A. F., 1866.*

One record (undated).

Rasahus albomaculatus (Mayr).

Rasahus albomaculatus Stal, *E. H., II, 1871.*

One record, 24. 7. 22. This example is a good deal smaller than that figured by Champion, but it appears to belong to this species, and Stal (*O. V. A. F.*, 1866) remarks that Mexican specimens are larger than those from South America.

Rasahus biguttatus (Say).

Rasahus biguttatus, Stal, *E. H., II, 1871.*

Two specimens dated May, 1922. Both flew into the laboratory lamps after nightfall.

Rasahus haematus (Fabr.).

Rasahus haematus, Champion, *B. C. A., Heteroptera II, 1901.*

A single example dated 5. 9. 20. The white band at the junction of the corium and clavus is confined to the margin of the corium.

Rasahus sulcicollis Serv.

Rasahus sulcicollis, Amy. Serv., *Hist. Nat. Ins. Hemipt.*

Two specimens obtained in July, 1922, seem to belong to this form.

Sirthenia stria (Fabr.).

Sirthenia stria, Stal, *H. F., I, 1868.*

This handsome species is quite common at Kartabo, and frequently flies into the lamps after nightfall.

Champion remarks that the outer half of the femora is more or less infuscate in specimens from Central America: this is also the case with those from Kartabo.

Mindarus basalis Stal.

Mindarus basalis, Stal, *E. H., II, 1871.*

Specimens from Kartabo agree fairly well with Stal's description of this species (type from Surinam), though he describes the colour as testaceous, whereas the examples in question are of a fine coral pink.

One specimen in the collection flew to the laboratory light after dark, 9. 6. 22: the others are undated.

Pothea lugens (Fabr.).

Pothea lugens, Stal, *H. F., II, 1868.*

This species has not yet been recorded from Kartabo. I took two examples on low herbage beside the Demerara River in October.

Zirta simillima Distant.

Zirta simillima, Distant, *Ann. Nat, Hist., X, 1902.*

I took one example on a young *Cecropia* tree in July.

Apiomerus hirtipes (Fabr.).

Apiomerus hirtipes, Champion, *B. C. A., Heteroptera, II, 1901.*

This insect is abundant in the forest round Kartabo Point, and varies considerably in colour. Some of the females have red genital appendages, abdominal expansions, and legs, while others are entirely black; but transitional forms occur, and no arbitrary distinction is possible. Likewise the males, which are smaller and of more slender build than the females, are often all black; but in some examples the femora-tibial articulations are flavous. Stal gives *A. hirtipes* Hahn, with black appendages, as a synonym of his species *nigrilobus;* but Champion does not admit this distinction, and I have followed his example and regard all these forms as varieties of *A. hirtipes* Fabr.

Apiomerus hirtipes is an active insect, but it is seldom seen upon the wing. The adults are often found crawling over timber infested with termites, or over the nests of these insects. They also hunt on foliage bordering the forest trails for other prey. I once saw one successfully impale a large black ant, transfixing it between the head and thorax. The nymphs, which are black with rufous femoro-tibial joints and sometimes with a reddish tinge on the dorsum, may be captured in termite galleries under bark, and in the younger stages are often clothed with vegetable debris. They are readily kept in captivity and their feeding habits can be studied under the microscope. When a termite is introduced into the cage, the bugs quickly become aware of its presence and show great excitement, vibrating their antennae and waving their forelegs. They then approach with deliberation, almost as if stalking their prey, and when close up they tread up and down as if groping with their feet. The antennae are not used to feel for the prey. When the tarsus has touched the termite, the bug instantly springs back to striking distance and thrusts forward rapidly with the proboscis. It then walks off leisurely with the victim impaled

on the rostrum. Sometimes two nymphs meet over the same termite. There is then great excitement—the antennae are flung back—the feet pound and stamp—and the hunters draw back with such ludicrous haste and commotion that the termite frequently eludes them both.

Calliclopius nigripes (Linn.).

Calliclopius nigripes, Stal, *H. F., 1868.*

This well-known and conspicuous insect, "la punaise vénimeuse" of Stoll, is common at Kartabo, and may be taken on foliage in the lighter forest trails.

Heniartes flavicans (Fabr.).

Heniartes flavicans, Stal, *H. F., 1868.*

This species has been taken several times at the Station.

Manicocoris rufipes (Fabr.).

Manicocoris rufipes, Stal, *H. F., 1868.*

This species has been taken at Kalacoon on the other side of the Mazzaruni River, but apparently not from Kartabo.

Micrauchenus lineolus (Fabr.).

Micrauchenus lineolus, Stal, *H. F., 1868.*

Fairly common at Kartabo in July and August, 1922. In every case the insects were resting on foliage in the trails and clearings at some height above the ground.

Acanthiscium superbus, sp. nov.

(Fig. 46, c).

Moderately stout, broad, rather pubescent; head, prothorax, mesosternum, scutellum, anterior femora, lateral expansions of the abdomen, and ventral aspect of the last three abdominal segments bright geranium red; remainder of body and legs, antennae, rostrum, tylus, and a median streak between the ocelli black; elytra black with violet reflections.

Head sub-quadrangular, unarmed, somewhat tumid behind the eyes; neck long and slender, eyes very large and prominent; first joint of the rostrum equal in length to the second and third together; antennae (broken) slender, shining.

Prothorax half as long again as the head and neck together, clothed with soft light hairs; anterior lobe with a small conical tubercle on either side of the neck and two low bosses separated by a longitudinal furrow on the disc; posterior lobe sub-pentagonal, with the outer edges carinate, and somewhat expanded, and produced upwards and outwards at the lateral angles; disc traversed by two carinae which arising from the bosses of the anterior lobe, diverge as they pass backwards and then converge behind, the curved part of each carina being furnished with six black-tipped spines, of which the first and the sixth are the longest and are vertical while those intermediate are short and diverge outwards; the disc bordered by the carinae is raised into a flat-topped eminence,

sloping in front, concave and declivous behind, and somewhat inflated so as almost to conceal the scutellum which is swollen and rounded at the apex.

Abdomen rather stout, slender at the base and widening to the fourth segment, then narrowing and truncate at the apex, lateral expansions of the abdomen somewhat pronounced and upcurved, unarmed. Legs not very long, the anterior pair stout, the other two pairs slender; the anterior femora greatly incrassate, furnished with a stout spine on the trochanter and almost as long as the hind-femora, the latter not reaching the apex of the abdomen.

Elytra ample, considerably longer than the abdomen.

Long. 22.0 mm. Lat. 8.0 mm.

Type: Female.

A single example of this beautiful species (undated) has been taken at Kartabo. The semicircular spined ridges on the disc of the posterior lobe of the pronotum are distinctive.

Debilia fraudulenta, sp. nov.

(Fig. 47, f).

Elongate, slender, body pubescent and the legs thickly clothed with longer stiffer hairs; fawn-brown, clouded with burnt orange on the upper surface of the abdomen; eyes red; elytra light brown; membrane and wings yellowish hyaline.

Head oblong, shorter than the prothorax, clothed below with long hairs, armed in front with two sharp stout spines; post-ocular portion somewhat swollen; eyes large, occupying the entire side of the head and with a deep transverse sulcus between them; ocelli prominent, set closely to the superior-posterior margin of the eyes; the first joint of the rostrum at least twice as long as the second and third together; antennae very elongated, the first joint more than twice as long as the second.

Pronotum granular, divided transversely by an obscure furrow; the anterior lobe small, narrow, rugose, non-tuberculate, with a deep median sulcus; the posterior lobe expanded, slightly inflated behind, furnished with two longitudinal carinae which terminate behind in short spines; lateral angles produced into rather long, outwardly directed spines; the posterior border emarginate, sharply reflexed above the scutellum which is rather large, triangular, and produced into a short stout tooth. Elytra not reaching the apex of the abdomen. Abdomen somewhat expanded at the sides, and with a pair of minute spines at the outer apical angles of segments 1–3. Legs long and slender, the hind pair the longest; anterior femora incrassate.

Long. 14 mm. Lat. 3.5 mm.

Type: Male.

Two examples obtained at Kartabo in September 1922. This form is very sluggish and lies on the upper surface of leaves in sunny places. The posterior legs and the antennae are laid back parallel with the long axis of the body, and the thickened anterior legs are folded and extended at right angles. The usual prey seems to be Jassid nymphs which are taken as they run over the leaves, but in captivity small flies are also eaten.

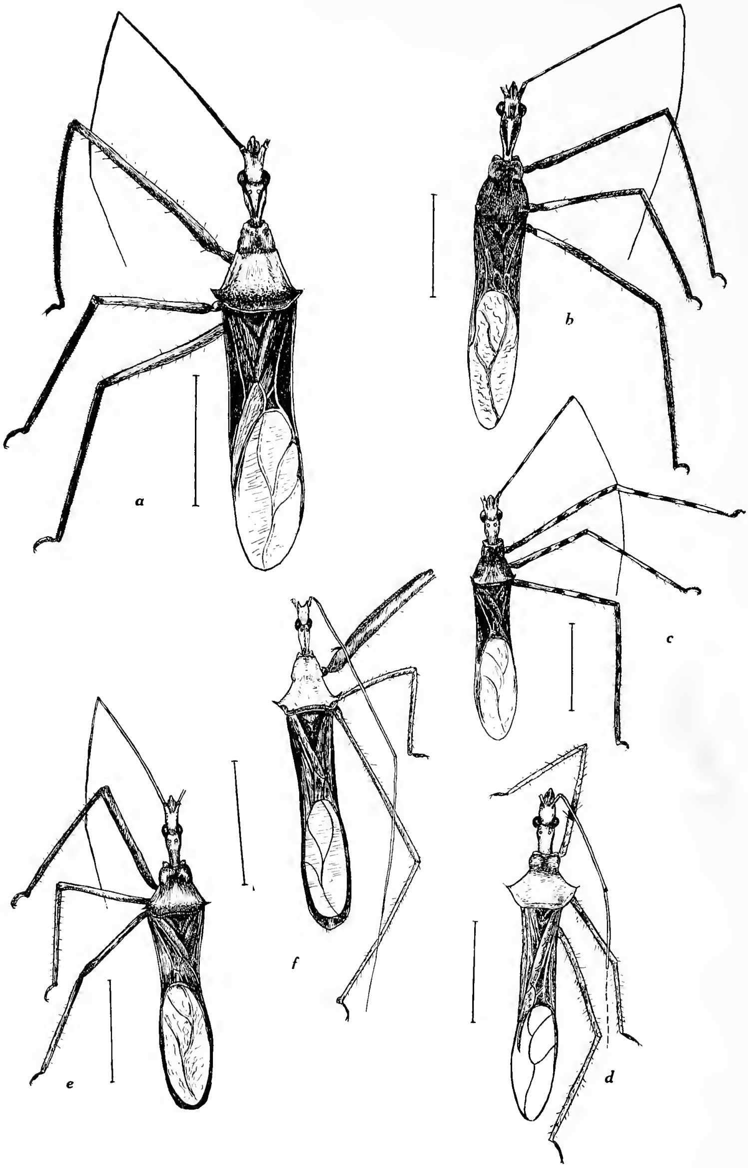


Fig. 17. *a*, *Zelus pallidinervus*; *b*, *Zelus kartabensis*; *c*, *Zelus araneiformis*; *d*, *Zelus formosus*; *e*, *Zelus rufigeniculatus*; *f*, *Debilia fraudulenta*.

Graptocleptes fasciata (Fabr.).

Graptocleptes fasciata, Stal, *H. F., 1868.*

A mutilated example dated 28. 8. 21. seems to belong to this form.

Notocyrtus dorsalis (Gray) var. *flavolineatus* Stal.

Notocyrtus dorsalis var. *flavolineatus*, Stal *E. H., 1871.*

Examples taken in July and September seem to be of this species though they vary a good deal in the amount of yellow on the posterior lobe of the pronotum.

Notocyrtus gibbus (Fabr.).

Notocyrtus gibbus, Stal, *H. F., 1868.*

This interesting species is quite common at Kartabo. It haunts clearings and open bushy places where it runs actively over the foliage. It is often found sucking nectar from the extra-floral nectaries of certain plants, or sipping honey-dew spilled by Coccids or Membracids.

Notocyrtus triareatus Stal.

Notocyrtus triareatus, Stal, *O. V. A. F., 1859.*

One example, dated June, 1920.

Montina testacea Stal.

Montina testacea, Stal, *E. H., II, 1871.*

Has been taken occasionally at Kartabo.

Repipta affinis, sp. nov.

(Fig. 46, f).

Moderately elongate, narrow, slender; head and abdomen glabrous, pronotum granular; legs and antennae with a few scattered hairs; the pleura and base of the corium clothed with a white agglutinated tomentum; pronotum dull rufus-brown; the rest of the body and elytra pale brown; the antennae darker.

Head scarcely as long as the pronotum and rather broad, tumid behind the eyes and much narrowed posteriorly; furnished with two minute blunt tubercles; antennae longer than the body and very slender.

Pronotum with two long slender spines on the disc of the posterior lobe, and from these two faint carinae extend forward to the transverse groove; lateral angles armed with shorter spines.

Scutellum rather large, pale, and toothed at the apex.

Abdomen unarmed, and not quite as long as the elytra.

Legs slender, hairy, especially the anterior pair which are slightly thickened at the base; the hind femora (when extended backwards) reaching the apex of the fifth abdominal segment.

Long. 10 mm. Lat. 2 mm.

Type: Female.

Two females taken by sweeping in August, at Kartabo and Kermaria Rapids respectively. This small inconspicuous species has much the facies of *R. mucosa* Champion, but differs in the shortness of the head spines and in other particulars.

Repipta flavicans Am. and Ser.

Repipta flavicans, Champion, *B. C. A., Heteroptera II, 1901.*

I took two examples, rather dark in colour, at Diamond Plantation (Demerara) in October, 1922.

Repipta mucosa Champion.

Repipta mucosa, Champion, *B. C. A., Heteroptera II, 1901.*

I obtained a single example in June by sweeping. The spines are slightly longer and the colour darker than the type.

Ricolla pallidinervis Stal.

Ricolla pallidinervis, Stal, *O. V. A. F., 1859.*

A common species, and there are records for nearly every month of the year. It frequents grassy open places, resting on the top of the herbage. When handled it emits a powerful but not unpleasant odour.

Sinea caudatum Champion.

Sinea caudatum, Champion, *B. C. A., Heteroptera II, 1901.*

I obtained a single example by sweeping beside the Demerara River in October.

Xystonyttus ichneumoneus (Fabr.).

Xystonyttus ichneumoneus, Stal, *E. H., 1871.*
Xystonyttus n. n. Cosmonyttus, Kirkaldy, *Can. Ent., 1909.*

Not uncommon at Kartabo, June–September. Specimens from this district have the head, basal and apical joints of the rostrum, antennae, prosternum, metasternum, coxae, femora, tibiae, tarsi, and the apex of the abdomen black; the pronotum, scutellum, metasternum, and proximal segments of the abdomen are bright orange red; the base of the second rostral joint and an annulation on the first and third pairs of femora are dirty white.

Xystonyttus nugax (Burm.).

Xystonyttus nugax, Stal, *E. H., 1871.*
Xystonyttus n. n. Myocoris Burmeister, and Cosmonyttus Stal, Kirkaldy, Can. Ent., 1909.

These Ichneumonid-like Harpactorinae are difficult to determine, especially as the types have often been described from what are evidently faded specimens. An example of this form from Kartabo has the thorax, underparts, and fore-femora bright orange yellow; the hind-femora are flavous with darker rings; and the ventral surface of the posterior abdominal segments is clouded with black.

Zelus (Diplodus) araneiformis, sp. nov.

(Fig. 47, e).

Elongate, moderately robust, rather hirsute; head pale castaneous red; pronotum pitchy brown, emarginated behind with pale testaceous; abdomen pitchy brown above, paler below, the first six segments decorated on each side with two white tomentose patches; elytra brown, with paler venation, rather longer than the abdomen; antennae and legs pale chestnut, conspicuously annulated with dark brown.

Head oval, pubescent, shorter than the thorax, somewhat swollen behind the ocelli; antennae longer than the body. Pronotum with the anterior lobe rough and sulcate; posterior lobe granular, pubescent, with two faint median carinae; depressed at the outer margin and with the lateral angles furnished with a very small forward-projecting yellow tooth. Scutellum bristly, triangular, depressed at the apex.

Legs rather long, equal in length, with scattered hairs.

Long. 10 mm. Lat. 2 mm.

Type: Female.

One taken on foliage at Kartabo, 9. 9. 22. The ringed legs and antennae are conspicuous and give the insect when in the resting position some resemblance to a spider.

Zelus erythrocephalus Fabr.

Zelus erythrocephalus, Stal, H. F., 1869.

The type of this species was a male, and two of that sex which agree very well with Stal's description were taken at Kartabo. Two females of this species, collected in June, resemble the males but are of larger size. In both sexes the anterior wall of the prothorax is ferruginous brown like the head. This insect, with others of the same genus, frequents sunny trails and clearings in secondary growth.

Long. Male: 13.0 mm. Female: 18.0 mm.

Lat. Male: 1.5 mm. Female: 2.0 mm.

Zelus (Diplodus) formosus, sp. nov.

(Fig. 47, d).

Somewhat robust, dull, coarsely granular; legs glabrous with a few scattered hairs; head and antennae fuscous, with a V-shaped mark behind the eyes and extending along the neck; pronotum apricot-yellow with a broad ill-defined band across the posterior lobe between the lateral spines; scutellum ochreus; abdomen yellow, with the last four tergites infuscate; legs yellow, with the tarsi and a ring round the femur dark brown; elytra yellow, with the clavus and membrane clouded with brown.

Head elongate, slightly tumid and then narrowing behind the eyes. Pronotum longer than the head; the anterior lobe rugose, sulcate down the middle, and with the anterior angles bluntly tuberculate; posterior lobe rough, with a very small lateral spine or tooth and the posterior border emarginate.

Scutellum sub-triangular, slightly toothed at the apex.

Elytra quite as long as the abdomen.

Legs rather short, the anterior femora a little longer but scarcely thicker than the posterior.

Long. 14 mm. Lat. 3 mm.

Type: Female.

A single individual taken on foliage at Kartabo in August. An unnamed example in the British Museum (collected by Bates in Santarem) differs only on the more distinct annulation of the femora.

Zelus (**Diplodus**) **kartabensis,** sp. nov.

(Fig. 47, b).

Moderately elongate, rather robust, dull, punctate, pitchy-brown, with patches of white tomentum on the underparts; head dilute ochreus, with a dark median patch in front of the eyes and two obscure streaks extending from the posterior margins of the eyes along the neck; rostrum and antennae black; sides of thorax and coxae, lateral expansions of the abdomen, a median line along the ventrum, the proximal two-thirds of the eighth sternite, and a ring at the base of the second and third pairs of femora, pale ochreus-green.

Head elongate, oblong, the post-ocular as long as the ante-ocular portion, neck cylindrical, ocelli rather prominent; antennae very long and slender, first joint a little thickened. Pronotum with the anterior lobe smooth, obscurely sulcate and tuberculate in front; the posterior lobe coarsely granulate with indications of two longitudinal diverging carinae; posterior border emarginate and somewhat produced over the scutellum; lateral angles toothed. Scutellum triangular, terminating in a small peg-like process. Eighth abdominal sternite large, boat-shaped. Elytra not quite as long as the abdomen. Legs long and slender, the anterior femora slightly incrassate and longer than the two posterior pairs.

Long. 13 mm. Lat. 3.0 mm.

Type: Male.

Four males of this form were taken by sweeping in Kartabo clearing in August. I cannot identify them by any published description and therefore describe them as new.

Zelus nugax Stal.

Zelus nugax, Stal, *Stett. Ent. Zeit., 1862.*

This species varies somewhat in the colour and the length of the spines. Two examples taken near Georgetown in October resemble slender short-spined Central American specimens. In life the dorsal surface of the abdomen and the underparts are chestnut, and the lateral expansions of the abdomen are dirty green; but these colours fade, and in any case they are variable. Three examples collected at Kartabo in July and August are much darker in colour, especially as regards the underparts and legs.

Zelus (Diplodus) pallidinervus, sp. nov.

(Fig. 47, a).

Elongate, moderately robust, dull, granular; head and prothorax clothed with very short stiff black hairs. Head green with a dark V-shaped mark behind the eyes; antennae and apical joint of the rostrum black. Prothorax apple-green with a transverse dark mark across the posterior lobe behind the spines. Scutellum and underparts green. Dorsum of the abdomen orange red, clouded with brown; lateral expansions of the abdomen green. Elytra testaceus with the corium and part of the clavus dark brown; veins broad and conspicuous, pale yellow. Femora pale green; tibiae and tarsi blackish.

Head oblong, elongate, antennae very long and slender. Prothorax with the anterior lobe sulcate and the anterior angles rounded; the posterior lobe faintly pilose, provided with two small lateral spines and with the posterior border emarginate. Scutellum triangular, terminating in a short tooth. Elytra just reaching beyond the apex of the abdomen. Legs long, the anterior pair considerably the longest; the anterior femora slightly incrassate.

Long. 17 mm. Lat. 3.5 mm.

Type: Female.

Four females were taken at Kartabo in August, on foliage in open places. This species is darker and more robust than *Z. laevicollis* Champion and differs from the description of *Z. sphegeus* Fabr. in the shorter thoracic spines, and in the conspicuous pale venation of the elytra which is its most distinctive character.

Zelus sphegeus Fabr.

Zelus sphegeus, Stal, *H. F.*, *1868*.

This pretty insect is fairly common at Kartabo on leaves in open bushy places. It is not unlike *Z. exsanguis*, but differs in the sculpture of the anterior lobe of the pronotum. Stal's description evidently applies to a dried specimen. In life the colours are: head and underparts yellowish-green; prothorax yellowish-green, marked behind the disc of the posterior lobe with black; dorsum of the abdomen rich chestnut orange; coriaceus portion of the hemielytra chestnut; antennae and legs black; the coxae and proximal third of the femora greenish-yellow.

Zelus (Diplodus) rufigeniculatus, sp. nov.

(Fig. 47, e).

Slender, elongate, not robust, rather hirsute; head and thorax purplish brown; dorsum of abdomen dull red with an indefinite median green line; underparts apple green; legs pale green with reddish femoro-tibial joints; antennae fuscous; ocelli red. Head oblong, with silvery pubescence, not quite as long as the pronotum; neck cylindrical and rather stout.

Pronotum with the anterior lobe with two somewhat pronounced tubercles at the anterior angles, sulcate in the middle and laterally decorated with white pilose lines and patches; posterior lobe punctate, rough, emarginate, faintly

bi-carinate on the disc and furnished at the lateral angles with two short black spines. Scutellum triangular, blunt, and slightly upturned at the apex. Elytra as long as the abdomen. Legs rather short, anterior femora a little swollen before the apex.

Long. 14 mm. Lat. 2.5 mm.

Type: Female.

Two examples taken at Canje Creek, Berbice, in October.

Zelus (**Diplodus**) **tristis,** sp. nov.

Slender, elongate, deep fuscous brown; head, margin of pronotum and lateral expansions of the thorax dull testaceus; an obscure V-shaped dark mark behind the eyes; antennae black; legs deep testaceus, ringed with black.

Head elongate, the ante-ocular portion much shorter than the post-ocular, a little tumid behind the eyes; ocelli prominent; pronotum with the anterior lobe smooth, dull, sparsely pubescent; sulcate in the median line, with the anterior angles rounded; posterior lobe coarsely granular and punctate, with two obscure median carinae; margins carinate and rather depressed; lateral angles armed with a very small tooth.

Scutellum pale, triangular, depressed at the apex.

Elytra rather longer than the abdomen, pale brown. Legs comparatively short; the anterior tibiae thickly, the posterior pairs more sparsely pilose; the anterior femora considerably the longest and slightly thickened at the base.

Long. 10 mm. Lat. 2 mm.

Type: Male.

A single example taken by sweeping in the forest in July. Superficially this species resembles a dark example of *Z. araneiformis* but differs from it in that the post-ocular portion of the head is more flattened, the thorax and the legs are more hairy, and the scutellum and anterior lobe of the thorax differ slightly in sculpture.

New York Zoological Society

Scientific Publication

		Paper	Cloth
ZOOLOGICA VOL. I			
Parts 1–20	*Not bound*	3.85	
Parts 1–20	*Bound*		6.00
ZOOLOGICA VOL. II			
Parts 1–18	*Not bound*	4.30	
Parts 1–18	*Bound*		6.50
Postage weight, 4 pounds			
ZOOLOGICA VOL. III			
Parts 1–23	*Not bound*	3.25	
Parts 1–23	*Bound*		5.00
ZOOLOGICA VOL. IV			
Parts 1–5	*Not bound*	2.35	
Parts 1–5	*Bound*		4.00
ZOOLOGICA VOL. V			
Parts 1–21	*Not bound*	1.90	
Parts 1–21	*Bound*		3.50
ZOOLOGICA VOL. VI			
Parts 1–5	*Not bound*	2.95	
Parts 1–5	*Bound*		4.50

All other volumes of Zoologica listed are not completed.

ZOOLOGICA VOL. VII

1—Three-Toed Sloth (*Beebe*)	.60
2—Development of Soldier Termites (*Emerson*)	.25
3—A New Polychaetous Annelid (*Treadwell*)	.10
4—A River Dolphin from Kartabo (*Williams*)	.30

ZOOLOGICA VOL. VIII

1—The Arcturus Expedition (*Beebe*)	.50
2—Arcturus: Equipment and Operation (*Tee-Van*)	.60
3—Brotulid Fishes (*Trotter*)	.20
4—Galapagos Brachyura (*Boone*)	1.40
5—Embryology of American Eel (*Fish*)	.30
6—Studies on Body-Forms of Fishes (*Gregory*)	.75
7—Annotated List of Synentogathi (*Nichols-Breder*)	.45
8—Polychaetous Annelids (*Treadwell*)	.30
9—Sea Stars from the Arcturus Expedition (*Fisher*)	.15
10—Scyphomedusae (*Bigelow*)	.25
11—Siphonophorae (*Bigelow*)	.65

	Paper	Cloth
ZOOLOGICA VOL. IX		
1—Marine Fishes—New York and So. New England (*Nichols-Breder*)	1.40	
2—Inquilinism (*Gudger*)	.15	
3—Frog Tagging (*Breder-Redmond*)	.30	
4—Turtle Trailing (*Ruth Breder*)	.25	
5—Functions and Morphology (*Parr*)	.25	
6—Uruguayan Fur-Seal Islands (*Smith*)	.25	
7—Field Observations on Flying Fishes (*Breder*)	.15	
8—Charles Island Tortoises (*Brown*)	.25	
9—Color Changes of Fishes (*Townsend*)	1.85	
10—The Blue-Spotted Sunfish (*Breder and Redmond*)	.25	
11—Chemical Control of Sea Water (*Breder-Howley*)	.35	
12—Fur Seal, California Islands (*Townsend*)	.60	
13—Growth and Age, Giant Tortoise (*Townsend*)	.25	
ZOOLOGICA VOL. X		
1—The Fishes of Port-au-Prince Bay, Haiti (*Beebe-Tee-Van*).	1.90	
ZOOLOGICA VOL. XI		
1—Haematology of the Camelidae (*Ponder-Yeager-Charipper*)	.15	
2—Haematology of the Primates (*Ponder-Yeager-Charipper*)	.15	
3—Direct Bone Formation in Antler Tines (*Noback-Modell*)	.60	
4—List of Antillean Reptiles and Amphibians (*Barbour*)	.40	
5—Digital Epiphyses, Carpal Bones, Infant Gorilla (*Noback*)	.90	
6—Great Smoky Mountains (*McClure*)	.30	
ZOOLOGICA VOL. XII		
1—Deep-sea Fish; Hudson Gorge (*Beebe*)	.50	
2—Haplophryne hudsonius (*Beebe*)	.50	
3—Notostomus beebei (*Boone*)	.15	
4—New Decapod and Isopod Crustaceans (*Boone*)	.25	
ZOOLOGICA VOL. XIII		
1-2—Bermuda Oceanographic Expeditions (*Beebe*)		

ZOOPATHOLOGICA VOL. I		
Parts 1-8	*Not bound*	2.05
ZOOPATHOLOGICA VOL. II		
1—The Treatment of Fish Diseases (*Mellen*)		.50

A completely classified list of the subjects included in each of the finished volumes of Zoologica, and all other publications of the New York Zoological Society will be furnished on application. Address H. R. Mitchell, Manager, Zoological Park, 185th St. & Southern Boulevard, New York City.

Index